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THE CONDOR

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TEMPERATURE REGULATION IN LAYSAN AND BLACK-FOOTED ALBATROSSES

By THOMAS R. HOWELL and GEORGE A. BARTHOLOMEW

This paper represents part of a more extensive study on the thermoregulatory responses of nesting sea birds to naturally occurring environmental conditions. Sea birds are especially suitable for such investigations as they may be found nesting in large concentrations in sites that are often fully exposed to the impact of the environment. Numerous procellariiform species offer such advantages for study, but there are relatively few data on thermoregulation in members of that order. Farner (1956) and Farner and Serventy (1959) have provided summaries of the pertinent literature. Our studies were conducted on Midway Island, latitude $28^{\circ} 13'N$ and longitude $177^{\circ} 23'W$, in the Leeward Chain of the Hawaiian Islands. Midway is a coral atoll consisting of two small islands—Sand and Eastern islands—and a fringing reef. It is a major nesting site for pelagic birds of three avian orders, and most of the species are present in great numbers. Furthermore, they exhibit to a marked degree the well-known tameness of birds that breed on remote oceanic islands. In consequence, one can obtain in rapid succession a series of measurements from large numbers of individuals exposed to virtually identical environmental conditions. As Midway has served as a cable station and as a naval base for many years, numerous observers have recorded much useful data on the breeding cycles and general natural history of the avifauna (see Bailey, 1952 and 1956, for recent summaries). All of these factors combine to make Midway a uniquely favorable place for studies such as the present one.

ENVIRONMENTAL CONDITIONS

The macroclimate of Midway Island is remarkably equable. Weather data from the navy meteorological station for the months pertinent to our observations are given in table 1; the air temperatures were taken at a height of 21 meters. The climate in January and February is the coolest to which the young birds are exposed; June and July cover the hottest period for juveniles still on land. The absence of stressful temperatures in January and February is noteworthy, as is the almost continuous wind during the warmer part of the year. Air temperatures taken at a height of 21 meters, however, are not always indicative of conditions in locations on or near the ground. In January and February the air temperatures we recorded at the nest sites of albatrosses were not notably different from those of the weather station. In June and July, however, in areas where juvenal birds were numerous, soil temperatures as high as $40^{\circ}C$. and black-bulb temperatures of almost $50^{\circ}C$. were recorded. Air temperatures above the maxima recorded at the weather station were noted almost daily.

The mean annual precipitation is 106 cm., and rainfall may occasionally be so heavy as to cause flooding and destruction of nests. Sandstorms caused by violent winds sometimes occur in winter and may destroy nests situated in exposed locations.

TABLE 1
SUMMARY OF WEATHER STATION DATA DURING WINTER AND SUMMER, RECORDED ON
SAND ISLAND AT A HEIGHT OF 21 METERS*

Month	Maximum	Minimum	Mean high	Mean low	Mean wind velocity	Per cent calm
January	24.5	13.0	21.0	17.0	12.8	3.5
February	24.5	12.0	21.0	15.0	12.2	3.0
June	30.5	18.5	28.0	21.0	8.7	2.7
July	31.0	19.5	28.5	23.0	9.3	2.5

*Air temperatures in °C.; wind velocity in knots.

MATERIALS AND METHODS

All measurements were made on unconfined birds under natural conditions. Temperatures were measured by means of a portable, battery-powered, multi-channel thermister thermometer manufactured by the Yellow Springs Instrument Company, Yellow Springs, Ohio. We used a variety of probes and leads that enabled us to measure temperatures with the sensing element as far as sixty feet from the indicating meter. All thermisters were calibrated with a Bureau of Standards thermometer. Temperatures were read to the nearest 0.1°C. By using several sensing elements in different channels of the instrument, we were able to obtain essentially simultaneous determinations of black-bulb, air, substratum, and body temperatures. Deep body (core) temperature was measured by gently inserting a steel-sheathed thermister probe down the esophagus to or into the stomach. Foot temperatures were obtained by enclosing a "banjo tip" surface-temperature-indicating thermister in a fold of the webbing. The same thermister was used in taking incubation patch temperatures by pressing the flat tip of the probe against the bare skin. Temperatures of unpipped eggs were obtained by slipping a vinyl-sheathed probe, 3 mm. in diameter, through a small hole bored in the shell; care was taken to place the thermister element in the approximate center of the egg. Temperatures of pipped eggs were measured by introducing the thermister through the punctured shell and pressing it firmly against the surface of the unhatched chick.

The albatrosses can be seized when on land without difficulty, and temperatures were recorded within 15 or 20 seconds after grasping the birds. It is highly improbable that any significant elevation of temperature due to struggle or excitement would occur in this brief interval.

LAYSAN ALBATROSS

The Laysan Albatross (*Diomedea immutabilis*) breeds primarily on islands of the Leeward Chain and ranges widely over the Pacific Ocean in the northern hemisphere. This species arrives on Midway about the first of November. Courtship and nest building begin, and eggs are present by the end of that month. The first young are hatched in late January, and they are constantly brooded by the adults for about two weeks. Feeding of the juveniles continues until July and August, when the young birds are finally able to fly. Both parents have an incubation patch and both participate in incubation, brooding, and feeding.

During our visit to Midway in January and February, 1960, we observed the late stages of incubation and the hatching and brooding of young birds. In June and July, 1959 and 1960, we observed full-grown juveniles not yet able to fly. At these times the young birds were unattended except for the feeding visits of the adults.

The Laysan Albatross is extremely numerous and widely distributed on both Sand and Eastern islands. It rarely nests on open, wind-swept sand but is partial to vegetated

areas such as *Casuarina* groves and *Scaevola* thickets. This species also nests abundantly among the buildings of the naval installations on the island. The nest is a raised bowl of sand about three to six inches high and includes bits of vegetation (fig. 1). The single egg or young chick is continuously brooded, and the parent may sit on the nest for many days before being relieved by its mate.

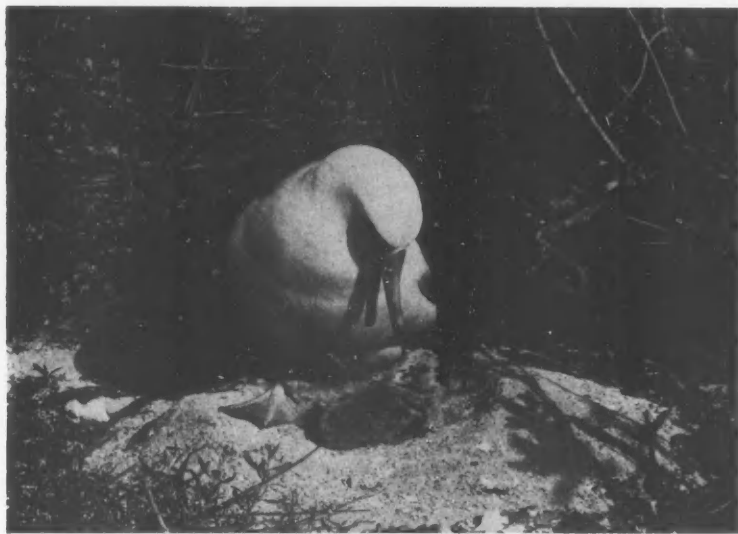


Fig. 1. Laysan Albatross (*Diomedea immutabilis*) with recently hatched chick.

We recorded body, incubation patch, and foot temperatures of brooding adults during the day and body temperatures at night. We also recorded under a variety of conditions the temperatures of eggs, recently hatched chicks, and large juveniles. The results are summarized in figure 2; noteworthy points are as follows:

1. Daytime body temperatures of brooding adults (mean 37.5°C.) average almost 1°C. higher than nocturnal temperatures, and the difference is statistically significant. The range of individual variation in body temperature is remarkably slight, and the means are lower than those usually reported for nonincubating individuals of other species.

2. Incubation patch temperatures (mean 36.7°C.) are significantly lower than body temperatures and much higher than foot temperatures (mean 26.9°C.) of adults. The feet clearly do not contribute to incubation heat in this species.

3. The temperatures of advanced brooded eggs (mean 36.0°C.) are not significantly different from incubation patch temperatures.

4. The temperatures of brooded, recently hatched young (mean 38.9°C.) are significantly higher than either incubation patch temperatures or body temperatures of brooding adults.

5. The body temperatures of large juveniles (mean 39.3°C.) exposed to intense solar radiation are much higher than the daytime body temperatures of unstressed brooding adults but lower than those of adults that have been active in full sun (mean 40.5°C.).

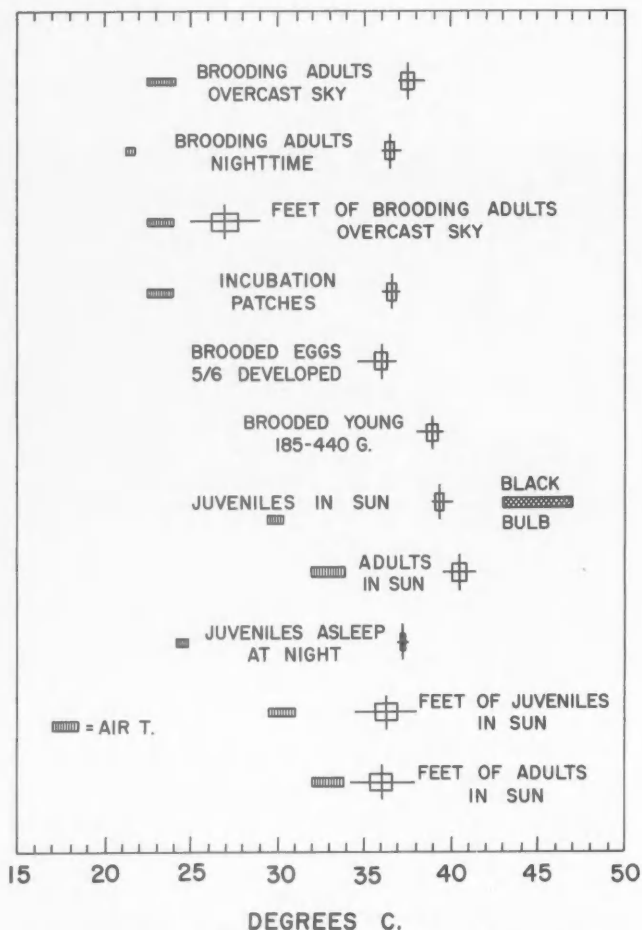


Fig. 2. Summary of temperature data for the Laysan Albatross. Horizontal lines indicate the range; vertical lines indicate the means (M); rectangles indicate the interval $M + 2\sigma_M$ to $M - 2\sigma_M$. In all cases sample size is 10.

6. Body temperatures of large juveniles asleep at night (mean 37.2°C.) are slightly higher than nighttime temperatures of brooding adults that are awake (mean 36.6°C.).

The foot temperatures of large juveniles require extended comment. During the summer months solar radiation may be intense, and the birds are often fully exposed to this stress. Under these conditions, body temperatures of juveniles are elevated about 2°C. above those of unstressed adults, but foot temperatures of juveniles are about 10°C. higher than those of unstressed adults (fig. 2).

Juveniles in the sun characteristically sit balanced on their heels with the webbed



Fig. 3. Juvenal Laysan Albatross resting on its heels. For photographic clarity the bird was induced to turn so that the feet were in the sun; the feet are usually kept in the shade of the body.

feet spread and held in the air (fig. 3). The birds almost always orient themselves with their backs to the sun so that their feet are in the shade of their bodies, even if this means facing away from the prevailing winds. Temperatures of feet held off the ground, as well as temperatures of the body, the air, and the substratum in the sun are given in table 2. The foot temperatures are always higher than those of the surrounding air but

TABLE 2
RELATION OF FOOT TEMPERATURES OF JUVENAL LAYSAN ALBATROSSES, EXPOSED TO
INTENSE SOLAR RADIATION, TO TEMPERATURES OF AIR AND SUBSTRATUM*

	Birds balanced on heels with feet in air	Birds crouched on soil with feet underneath body
Air	29.4-31.0	31.0
Substratum	39.5-40.2	31.0-36.1
Foot	36.3 ± 1.1	36.9 ± 0.6
Body	39.3 ± 0.8	39.3 ± 0.8

*Data from 11 birds with feet exposed and 10 birds with feet sheltered.
Temperatures in °C.

lower than those of the substratum. It follows that heat is lost from the feet by radiation and convection to the cooler air, whereas heat would be gained by conduction were the feet rested on the hot substratum.

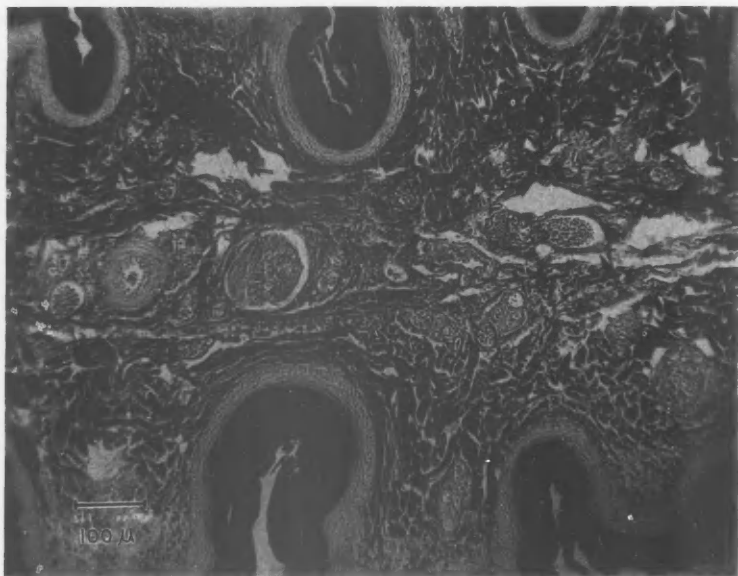


Fig. 4. Photomicrograph of foot webbing of juvenile Laysan Albatross, showing heavy vascularization. Mallory Azan stain was used.

In some cases, juvenile birds exposed to intense solar radiation remained crouched on the substratum with the feet kept under the body. Temperatures of the feet and the shaded substratum under such birds are given in table 2. The foot temperatures are about the same as those of birds with feet exposed, but the substratum temperature is always lower than that of the feet. Hence, heat is lost by conduction from the feet to the cooler substratum.

These observations indicate that the feet function in heat loss as follows. Some juveniles do not move from the spot where they roosted at night until many hours after dawn, if at all. The substratum under these birds remains relatively cool as it is shielded from the sun, and as long as the feet are kept on this substratum they will lose heat to it. On the other hand, birds that move away from their roosting place may come to rest on a heated substratum, and when these birds settle down they assume the feet-in-air position. This odd posture has been noted by observers for over half a century (Fisher, 1903:18, pl. 5); it may serve some function in addition to permitting heat loss, but the latter must certainly occur. The foot temperatures of nonbrooding adults in the full sun are approximately the same as those of juveniles under the same conditions, but only one of many thousands of adults which we have observed assumed the feet-in-air posture so typical of the young birds. Presumably the adults need only take to the air to dissipate excess heat.

Samples of foot webbing of large juvenile Laysan Albatrosses were taken for histological examination. As shown in figure 4, there is considerable vascularity in the sub-epithelial tissue. There are larger vessels in the central part of the webbing and bundles of smaller ones near the surface of each fold of the skin; this arrangement would greatly

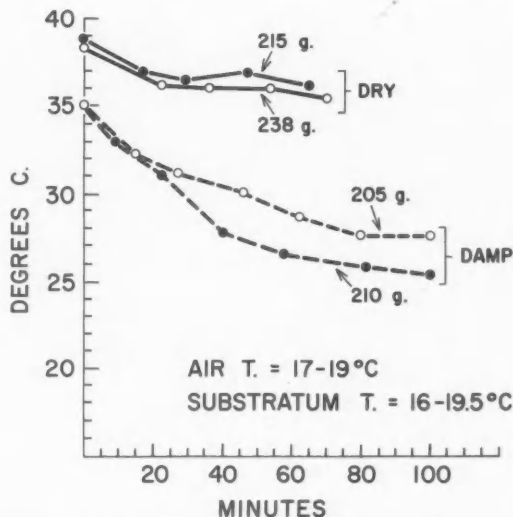


Fig. 5. Temperatures of newly hatched, unbrooded Laysan Albatrosses in shade.

facilitate heat loss to the environment. As expected, there is a high degree of vasomotor control in the foot webbing. When we attempted to obtain blood samples by cuts across visible blood vessels in the foot webs of juvenal albatrosses, we were usually unable to obtain even enough blood for a smear without vigorous "milking" or waiting as long as several minutes for some vasodilatation to occur. No amount of extensive cutting produced a copious flow of blood.

Like many other birds, albatrosses routinely employ evaporative cooling in regulating body temperature. Under conditions of severe heat loading both adults and young pant heavily with mouth open and throat lowered and distended, but they never show the gular fluttering so typical of pelecaniform birds. The panting rate is only moderately high and averages about 160 per minute (range shown by 10 heavily panting large juveniles in full sun, 138 to 198 per minute). When panting, the oral mucosa is conspicuously moist and drops of fluid commonly are visible in the corners of the mouth. Large juveniles often combine panting with the feet-in-air posture when they are exposed to intense solar radiation and little or no air movement.

As previously indicated, recently hatched and brooded young have higher temperatures than either brooded eggs or brooding adults. Obviously, the chicks are producing heat in addition to that provided by the parent. However, their heat-producing capacity is not sufficiently developed to permit the degree of body temperature regulation that is possible at a later stage. Figure 5 presents data on young chicks exposed to ambient temperatures lower than those provided by brooding adults. Two still-damp nestlings showed a steady decline in body temperature, finally leveling off about 10° to 12°C. below the initial brooded temperature and about 6° to 8°C. above the moderate ambient temperature. On the other hand, chicks of similar size but with dry down had a higher initial brooded temperature; after a small decline, they maintained a body temperature only slightly below that of adults under the same conditions. As the damp chicks were



Fig. 6. Black-footed Albatross (*Diomedea nigripes*) and its egg, at edge of *Scaevola* thicket.

only a few hours younger than the dry ones, we interpret the difference in regulatory capacity to be a function of quality of insulation rather than a difference in physiology.

BLACK-FOOTED ALBATROSS

The Black-footed Albatross (*Diomedea nigripes*) breeds on many Pacific islands between 10° and 30°N latitude and ranges over most of the Pacific Ocean in the Northern Hemisphere and into the Bering Sea. This species arrives on Midway in mid-October, about two weeks earlier than the Laysan Albatross. The breeding cycle closely parallels that of the latter species but is about two weeks in advance. Our observations on *D. nigripes* cover the same stages as mentioned for the Laysan Albatross.

The Black-footed Albatross nests commonly on both Sand and Eastern islands but is much less abundant than the Laysan Albatross. *Diomedea nigripes* tends to nest on open, wind-swept sand as well as among the bushes and trees, but it seems to avoid human habitation more than does *immutabilis*. Both forms, however, are often found nesting side by side in a randomly distributed manner. The nest of *nigripes* is generally lower and shallower than that of *immutabilis* and often consists only of a depression in the sand (fig. 6). Incubation of the single egg and the brooding behavior are essentially the same as in *immutabilis*.

We recorded body, incubation patch, and foot temperatures of brooding adults during the day and body temperatures at night. We also recorded temperatures of advanced eggs, pipped eggs, chicks of various ages, and large juveniles. The results are summarized in figures 7 and 8; noteworthy points are as follows:

1. Daytime body temperatures of brooding adults (mean 38.1°C.) under overcast skies average 1°C. higher than nocturnal body temperatures and the difference is statistically significant.

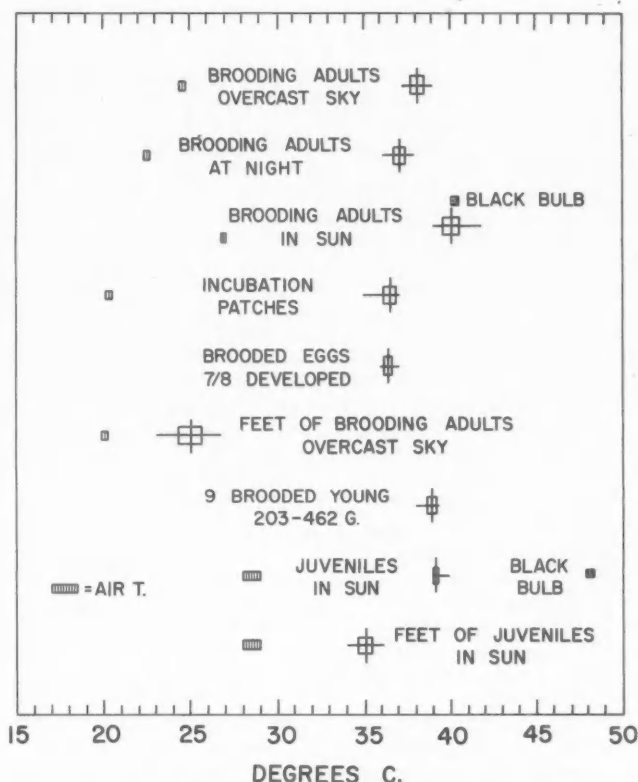


Fig. 7. Summary of temperature data for the Black-footed Albatross. For explanation of symbols see figure 2. Sample size is 10 with one exception as noted.

2. Brooding adults exposed to full sun have body temperatures (mean 40.1°C.) averaging 2°C. higher than those of birds not under heat stress.

3. Although the samples of adult body temperatures under given conditions are impressively uniform, the overall range of deep body temperatures covers 5.5°C.—from 36.2°C. (night) to 41.7°C. (sun).

4. Incubation patch temperatures (mean 36.6°C.) are virtually identical with the temperatures of advanced brooded eggs (mean 36.4°C.).

5. The feet do not contribute to the heat of incubation.

6. Temperatures of brooded, recently hatched young (mean 38.8°C.) are significantly higher than temperatures of the incubation patch or body temperatures of unstressed, brooding adults.

7. The body temperatures of large juveniles (mean 39.2°C.) exposed to intense solar radiation are much higher than the body temperatures of unstressed brooding adults. They are not as high, however, as those of brooding adults exposed to heat stress even though the heat stress was less for the adults than for the juveniles.

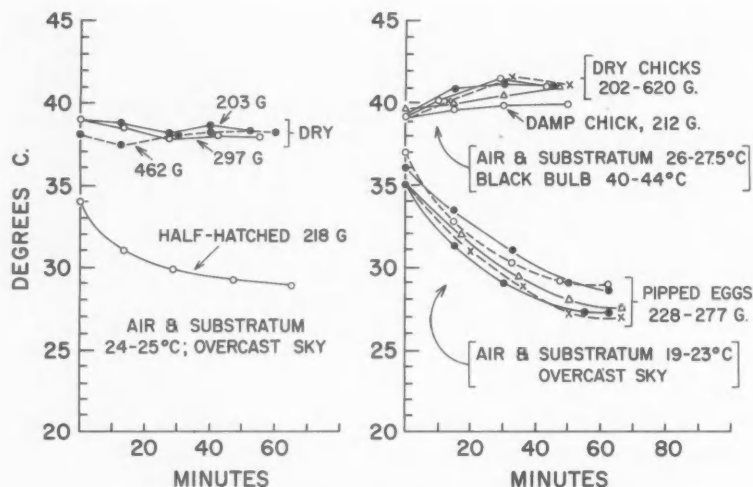


Fig. 8. Temperatures of unbrooded pipped eggs and unbrooded chicks of the Black-footed Albatross under various conditions.

8. Large juveniles under heat stress with feet raised in the air had foot temperatures (mean 35.1°C.) that were always higher than air temperatures (28°-29°C.). Presumably the role of the feet in heat exchange is the same as that discussed with regard to the Laysan Albatross. Panting rates and the use of evaporative cooling by *nigripes* also appear to be the same as in *immutabilis*.

Temperatures of pipped eggs taken from nests and exposed to moderately cool ambient temperatures showed a steady decline to a point about 6° to 8°C. above that of the environment and leveled off thereafter (fig. 8). Damp, newly hatched chicks of both *nigripes* and *immutabilis* under similar conditions showed essentially the same pattern. However, dry hatchlings at the same ambient temperature as damp ones showed a very slight initial decline and then stabilized their body temperature at about 38°C. (fig. 8). The mean for adults under similar circumstances is approximately the same.

When dry chicks of various ages (weights 202 to 620 gm.) were exposed to moderate heat stress, the pattern of response was surprisingly uniform (fig. 8). There was a slight initial rise in body temperature and then a leveling off; all stabilized at 41°C. This is within the range of adult temperatures under similar heat stress but is significantly higher than that of large juveniles under more severe conditions. The downy chicks began to pant soon after being exposed to the hot sun, but the feet-in-air posture used by the large juveniles was not employed.

A single damp hatchling was exposed to the same heat stress as the other young ones just discussed. Its initial body temperature was about the same as the others and the shape of its temperature curve is similar, but the body temperature remained slightly lower than that of the dry chicks and stabilized at about 40°C. instead of 41°C. Presumably this difference was the result of cooling by evaporation of moisture from the wet down and skin. It is of interest that the same factor that makes for poor regulation under cool conditions is helpful in preventing overheating under moderate heat stress.

The interpretation of the role of down in temperature regulation in the chick of the

Laysan Albatross is further supported by the data on the species discussed here. Under cool conditions, damp hatchlings do not show any improvement in temperature regulation over those still in the pipped-egg stage. Dry hatchlings, although insignificantly "older" and in some cases weighing less than the damp ones with which they are compared, show a vast improvement in regulatory capacity and under moderate environmental conditions maintain body temperatures close to those of adults.

Large juveniles that are hatched in entirely exposed nests on open sand face severe heat stress in the summer. During the hotter parts of the day, many or most of them retreat into dense *Scaveola* thickets where they are shaded from the intense sun. Some, however, are too far from such shelter and must depend entirely on their physiological capacity for heat loss in order to regulate body temperature.

DISCUSSION

On Midway Island these two congeneric species show slight differences in the timing of reproduction and in nest site preference, but there is much overlap in both of these aspects of their breeding activity. These albatrosses are similar in the physiological characteristics that we were able to study, and we could detect no evidence of significant differences in adaptations influencing temperature regulation under natural conditions. During January and February, the time of hatching and of the early nestling stages of these species on Midway Island, the climate is generally equable and mild. Occasionally there may be flooding rains or sandstorms caused by high winds, but apart from these exceptional and irregular conditions the early nestling period does not coincide with any severe environmental stress. Whether or not the dry, newly hatched chicks could regulate body temperature under conditions of greater stress as adequately as larger and older chicks do is uncertain. The ability to regulate body temperature well under rigorous conditions is almost never required of very young nestlings because of the moderate climate and the behavior of the parents. The eggs and the young chicks are normally closely brooded at all times, and only the adult birds meet the stress of the macroclimate. The effective environment of the egg or hatchling is actually a dry, shaded chamber kept at about 36°C. Even moderately heavy and sustained rains do not penetrate into the concavity of the nest although the sand surrounding the brooding adult may be thoroughly soaked. The strong attachment of the parents to their nest, as exemplified by the continuous brooding for days or weeks and by the reluctance to give place to the mate except after a prolonged change-over ceremony, insures that the egg or hatchling is well protected during its most critical period.

After the young birds become too large to be brooded, they are sufficiently well insulated and physiologically adequate to withstand all but exceptional environmental stress. With the advent of intense solar radiation in summer, the juveniles are able to lose enough heat through panting and by way of the foot webbing to maintain body temperature within quite narrow limits. The rapid panting of young birds in the sun undoubtedly results in considerable water loss. The food (mostly squid) provided by the parents has a high water content but it is virtually isotonic with the sea. The water in the body fluid of the squid, although highly saline, is physiologically available since the excess salt is excreted by the nasal gland (Frings and Frings, 1959). We often noted fluid dripping from the bills of juveniles. Thus, although the nonflying young birds never drink, they are provided by their diet and salt-excretion mechanism with enough water for both metabolic reactions and evaporative cooling.

It is now known that the adult birds drink sea water and indeed require salt to maintain good health (Frings and Frings, *op. cit.*). There are often puddles of fresh water

present on Midway Island immediately after rains, but we never saw any albatrosses attempt to drink from such sources. However, adult birds sitting on nests will nibble and snap at falling raindrops when a shower passes over. It is a remarkable sight when hundreds of incubating birds almost simultaneously begin catching raindrops as a squall reaches the island. We interpret this as a response to a long period of deprivation of food and water associated with long-continued brooding.

The mechanism of heat loss through the feet, although advantageous to juveniles on land and to adults in flight, could bring about excessive cooling when the feet are immersed in the sea. Even in the tropics the temperature of sea water is much lower than that of the bird, and the cooling power of water is 20 to 50 times that of air at the same temperature (Scholander, 1955). Excessive heat loss by way of the feet is doubtless minimized by vasomotor control. It is not known if albatrosses have tarsal arterio-venous *retes* which could provide a counter-current heat exchange system (Scholander, *op. cit.*) for heat retention when the birds rest on the open sea.

The nesting areas of albatrosses, like those of many other pelagic birds, are largely restricted to islands that are free of native terrestrial predators. Such islands, however, are usually predator-free because of their remote location and/or ecological conditions under which most terrestrial vertebrates could not become permanently established. Severe conditions that help to insure an absence of predators nevertheless pose serious problems for the birds that must tolerate the environmental stress if they are to nest successfully.

The large size of albatrosses and their specialized mode of flight are associated with a prolonged period of growth and development, and the duration of incubation and parental care spans three seasons of the year. This circumstance poses great potential difficulties for the birds. Either (1) they must avoid nesting in areas with extremes of seasonal climate, or (2) they must be adequately adapted at all stages of development to the stresses of such an environment, or (3) they must strike a balance between these two ways of meeting the problem. The two species of albatross discussed here demonstrate such a balance. They breed in a region where severe low temperatures do not occur. The timing of the reproductive cycle is such that the chicks hatch in a period of mild temperature, and by the time the extremes of summer heat are reached the young birds are well grown and the adults no longer need to brood. During this period of climatic stress, the physiological and behavioral mechanisms for heat loss enable adults and juveniles to regulate adequately their body temperature. A recognition and analysis of these mechanisms is therefore essential in the interpretation of the ecology and distribution of the species.

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SUMMARY

Temperatures of eggs, chicks, juveniles, and adults of Laysan (*Diomedea immutabilis*) and Black-footed (*Diomedea nigripes*) albatrosses were measured under a variety of environmental conditions on Midway Island.

Daytime body temperatures of brooding adults (means: *immutabilis*, 37.5°C.; *nigripes*, 38.1°C.) average about 1°C. higher than nocturnal body temperatures.

Incubation patch temperatures (means: *immutabilis*, 36.7°C.; *nigripes*, 36.6°C.) are significantly lower than body temperatures and are essentially the same as the temperatures of advanced brooded eggs.

The temperatures (means: *immutabilis*, 38.8°C.; *nigripes*, 38.9°C.) of brooded, recently hatched young are significantly higher than either incubation patch temperatures or body temperatures of brooding adults.

The body temperatures of juveniles and adults are elevated by exposure to intense solar heat. Under such conditions the birds pant vigorously, and the juveniles often sit balanced on their heels with their feet off the ground. This posture permits heat loss from the vascularized foot webbing to the air.

Temperatures of pipped eggs and damp, newly hatched chicks exposed to an ambient temperature between 21° and 23°C. decline to about 6°C. above that of the environment. Dry, newly hatched chicks at the same ambient temperature maintain a body temperature of about 38°C. The greater capacity for body temperature regulation in the latter group is attributed to more effective insulation.

The climate of Midway Island is generally mild and the birds are never exposed to severe cold stress. The timing of the breeding cycle is such that the young birds are well grown before the onset of summer heat. Physiological and behavioral adaptations to heat stress and their relation to the ecology of the two species are discussed.

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HELPERS AMONG BIRDS

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Twenty-five years ago, I published a paper (1935) on "Helpers at the Nest," in which I gave short accounts of the breeding of three species of birds whose nestlings were attended by individuals other than the two parents. In addition, I mentioned one other species in which I had found a helper and a few instances of similar behavior that had come to my attention in books. In the quarter-century that has elapsed since this paper was written, I have watched helpers of 16 additional species, and scores of similar instances have been described in print.

The purpose of the present paper is to give a comprehensive survey of the occurrence of helpers among birds, indicating the range of their activity and analyzing the circumstances that promote it. The first part contains a general discussion of the subject, and this is followed in the second part by a systematic list of instances of helpers known to me. This listing of cases which have come to my notice over the years does not pretend to be complete. Although most of the examples presented come from ornithological books and journals, others were found in books of a more general nature, in popular magazines of natural history, and even in the daily press. I doubt if I have noticed a third or even a quarter of the helpers which have been reported in print in all parts of the world. However, I believe that the examples cited give a fair notion of the range and variety of helpfulness among birds and indicate the groups and the circumstances in which helpers are most likely to be found.

To avoid needless duplication, I have omitted scientific names and citations of literature in the first part of this paper whenever these are to be found in the Annotated List which immediately follows.

THE STATUS AND ACTIVITIES OF HELPERS

Status of helpers.—A "helper" is a bird which assists in the nesting of an individual other than its mate, or feeds or otherwise attends a bird of whatever age which is neither its mate nor its dependent offspring. Helpers may be of almost any age; they may be breeding or nonbreeding individuals; they may aid other birds of the most diverse relationships to themselves, including those of distinct species; and they may assist in various ways. Hence the complete analysis of this subject involves attention to three questions: (1) The status or condition of the helper, whether young or old, a parent or a nonbreeder; (2) its relationship to the bird or birds which it assists; and (3) the activities in which it engages.

Although we commonly distinguish immature birds from breeding adults, there is, in many species, an intermediate group for which we lack a convenient designation because this class of individuals is not found in man and because our language developed with special reference to ourselves and our activities. Humans and other familiar mammals are, as a rule, able to reproduce before they cease to grow, often while they are far below their adult size. Many kinds of birds which are fully grown in one or a few months must wait almost two years, or in some species much longer, before they are ready to breed. Thus they pass through one or more nesting seasons, subsequent to that in which they hatched, without themselves nesting. To designate these intermediate individuals, we often use a phrase of several words, such as "full-grown, sexually immature individual."

To fill this gap in our nomenclature, I propose the term *innubile* (the negative of the Latin *nubilis*—marriageable) to designate birds which in a breeding season subse-

quent to that in which they hatched are still sexually inactive. We have, then, the following developmental stages in the life of a bird:

1. Nestling, from hatching to leaving the nest.
2. Fledgling, in nidicolous birds, or chick, in precocial birds, from leaving the nest to the cessation of parental care.
3. Immature, from the attainment of independence to the approach of the following breeding season. The bird may also be designated as juvenile while in the early part of this stage and while still bearing most of its juvenal plumage.
4. Innubile, from the beginning of the breeding season following hatching to the attainment of reproductive activity. Many small birds, which mature in a year or less, omit this stage, passing directly from the immature to the adult stage.
5. Adult or, if one wishes, "nubile"—mature individuals engaged in breeding or fully able to reproduce. Although in many small species innubiles are lacking, in numerous sea fowl and other larger birds, and even in some passerines, they form a large proportion of the total population.

Classification of helpers.—Helpers fall into two great classes with regard to their relationship to the birds they assist. There are "intraspecific helpers," who aid others of their own kind, and "interspecific helpers," who assist individuals of different kinds. With these distinctions, we may attempt a classification of helpers:

- I. In reproductive activities
 - A. Intraspecific helpers
 1. Immature helpers
 2. Innubile helpers
 3. Adult helpers
 - a. Nonbreeding adult helpers
 - b. Breeding helpers
 - Unilateral helpers
 - Mutual helpers
 - B. Interspecific helpers

The subdivisions under this heading are theoretically the same as under A, but actual records are lacking for some of them.
- II. In non-reproductive activities
 - A. Intraspecific helpers
 - B. Interspecific helpers

(The examples under both A and B that are at present available are so few that no subdivision seems advisable.)

Ways of helping.—The most common way in which birds help each other is by sounding the alarm at the approach of danger and by repelling animals of all kinds that intrude upon the nesting area. The warning cry which an alert bird raises when a hawk appears is recognized and heeded by individuals of other species, which dive into sheltering vegetation or try to escape detection by immobility. A hush falls over the countryside until the dangerous raptor passes. Indeed, not only do birds warn each other, they sometimes alert mammals that have learned the meaning of the cries or the attitudes of the birds frequently associated with them (Riney, 1951). Birds whose nests are close together, whether of the same or of different species, sometimes unite in threatening or attacking dangerous trespassers; or, more rarely, they try to lure them away by simultaneous distraction displays (Skutch, 1954-1955:563-564). Since helpfulness of this sort (other than the simultaneous distraction displays) is so common, and since it may be unintentional (each bird trying merely to deflect the intruder from its own nest or young), we shall say little about it in the remainder of this paper.

The next most common mode of helpfulness among birds is in feeding. Since the survival of most species depends upon the parents' placing sufficient food into the mouths of their young, the urge to give food to other individuals has become very strong in birds. It is one of the first forms of parental behavior to become manifest in the young and it has been observed even in nestlings. It persists in parent birds who have lost their young hours or even days earlier (Skutch, 1956:364). It has acquired importance in relationships other than parental, especially in courtship and maintaining the bond between mates, and in nourishing the incubating female. It turns up in the most unexpected contexts, as in the captive Raven which passed food through the bars of its cage to a free Black Vulture (*Coragyps atratus*), the Cardinal which fed goldfish, and the Jackdaw which, regarding Dr. Konrad Lorenz as his mate, pushed food into that ornithologist's mouth or even into his ear (Lorenz, 1952:136). Finally, it is one of the last modes of parental behavior to disappear when a species becomes parasitic and depends on others to rear its progeny; there are a number of recorded instances of the feeding of the young of their own kind by parasitic cuckoos (Moreau, 1944) and cowbirds (Bent, 1958:441, 462).

Less frequent forms of helpfulness are nest building, incubation, and brooding. In mature birds, building usually leads to laying and incubation; hence helpers who assist in nest construction generally belong to the class of "mutual helpers," who build, lay, and incubate with other individuals of the same or sometimes different species. There are, however, a few records of immatures or even nestlings helping to build or maintain the nest, as in European Cormorants, Crowned Hornbills, and Barn Swallows. Immature birds who feed nestlings not infrequently brood them, as in the Black-shouldered Kite, Eastern Bluebird, and Purple Martin mentioned beyond. There is even a record of a month-old Rock Dove attempting, not very successfully, to incubate the eggs of his mother's next brood. But most instances of the incubation of other birds' eggs or the brooding of their young by mature individuals fall under the heading of "mutual helpers."

Crèches.—One mode of helpfulness that was reported by earlier observers has not been substantiated by the most careful recent studies. In a number of species that breed on the ground, usually in colonies, the young, after they leave the nest and move around somewhat freely, gather into "crèches," where the offspring of several or many parents are mixed together and guarded by some of the adults while others go off to forage. Such aggregations of young birds have been described in penguins of several kinds, in flamingos, in eider ducks, and in the Sheld-duck, *Tadorna tadorna* (Coombes, 1950:409). In the latter the downy young of several parents form a flotilla on the water. It was formerly believed that in these nurseries the parents fed the young indiscriminately, rather than each his or her own. That each parent feeds its own offspring and not others, even when the young of many families are mixed together, has been demonstrated, or at least made probable, by the observations of Sladen (1953; 1955:245) on the Adelie Penguin (*Pygoscelis adeliae*) and the Chinstrap Penguin (*P. antarctica*), by Prévost (1955:251) on the Emperor Penguin (*Aptenodytes fosteri*), and by Brown (1958:410-412) on the Greater Flamingo (*Phoenicopterus antiquorum*). The parent Adelie Penguins studied by Sladen fed strange chicks only in exceptional circumstances.

A little reflection makes it clear that the indiscriminate feeding of the young by the parents, which at first glance appeals to us as an admirable mode of cooperation, would hardly be practicable without a degree of regimentation of the young which birds could hardly achieve, and which would be difficult even with human children in the open air. Unless the young penguins, flamingos, or other birds in the crèches lined up to receive their meals in turn, the largest and most aggressive of them would take more than their

share, and the smaller and more timid would go hungry. The system of individual attention to its own young by each parent insured that even a broken-winged young flamingo received its meal, although in a general melee to get food it would probably have lost out (Brown, *loc. cit.*).

Relative frequency of intraspecific and interspecific helpers.—Although there are many recorded instances of birds feeding or otherwise assisting members of distinct species, this form of helpfulness appears to be far less common than that which is given to other birds of the same species. In 30 years of bird watching in Central America, I have discovered intraspecific helpers at or near 31 nests of 18 species. No less than 55 individuals of these species were serving as helpers. I have excluded from these figures the communal nests of the anis and the mutual helpers that I watched there, because I knew beforehand of their peculiar breeding habits and made a special effort to study them. All the other helpers that I found were unexpected discoveries. As against this total of 55, I have seen only two individuals of two species—the Tropical Gnatcatcher and the Blue Honeycreeper—helping birds of different kinds. In the records of helpers published by others, interspecific helpers figure far more prominently, accounting for nearly 40 per cent of the reports that refer to free birds. If the computation were made on the basis of the number of individual birds serving as helpers, the percentage of interspecific helpers would be smaller but still quite substantial. But we should bear in mind that interspecific helpers are more likely to be noticed and reported by the casual bird watcher than are the intraspecific helpers. It usually requires sustained and careful observation to learn how many individuals of the same kind are attending a nest, but anyone who notices a bird feeding an individual of another species, or sharing a nest with it, is interested by the extraordinary occurrence.

Immature intraspecific helpers.—The Annotated List contains records of about 20 species in which free young birds of early broods helped with later broods in the same year, and a number of instances of helpfulness by captive immatures are also given. The groups in which immature or juvenal helpers have been most frequently observed are the Common or Florida Gallinule, Barn or European Swallow, House Martin, fairy wrens of Australia (*Malurus* spp.), bluebirds of North America (*Sialia* spp.), and Golden-masked Tanager. The activity in which these young birds most often engage is feeding nestlings and removing their droppings. On rare occasions they help, mostly rather ineffectually, to build, as has been witnessed in the Barn Swallow and the Red-throated Ant-Tanager. Sometimes they toy with building material but seem not to know what to do with it, as I have seen in the Golden-masked Tanager. Their dedication to their self-imposed task of feeding the nestlings is likely to be sporadic, spurts of activity alternating with periods of neglect, so that the nestlings would fare badly but for the steadier application of their parents. Juveniles may even brood, as in the Rock Dove, Purple Martin, and Eastern Bluebird; but this appears to have been observed only in captive birds.

Although in an aviary immatures may attend unrelated younger individuals of their own species and even nestlings or fledglings of different species, in the free state they seem usually to feed their younger brothers and sisters. Hence we should expect to find immature helpers chiefly in species which rear two or more broods in a single nesting season. Moreover, they are likely to occur only in the more sociable species, which do not, in the manner of many birds, repel the young of their previous brood as they prepare for the following brood or when this later brood hatches. When a young Cardinal brought food to a late nest, the female parent tried to drive it away, although the male was more tolerant.

Perhaps an unusual degree of precocity is also necessary to make helpers of the immature individuals of some species. In the family of Southern House Wrens whose fortunes I followed carefully for two years, the parents seemed to be more vigorous in the second year, when they began to breed exceptionally early, and their offspring likewise appeared to be more precocious in the second year. Although young Southern House Wrens are usually driven away about the time the following brood hatches, the first brood of the second year stubbornly refused to be evicted, and soon they were feeding the single nestling which remained from the four eggs of the second brood. With this assistance in the care of the second brood, the parents began to build a nest for the third brood. This was the only instance of this overlap of nestings that has come to my attention in this species. Even while building the third nest, the parents continued to bring food to the nestling of the second brood. But the young female helper, only 73 days old, became antagonistic to her mother and tried to keep the latter out of the gourd that sheltered the nestling. This gave rise to the fiercest struggle that I have ever witnessed among birds, in which the precocious young female was defeated and driven away. Her more pacific brother continued to feed the nestling.

Frequently young helpers, who have not completely outgrown their infantile ways, solicit food from their parents, then pass it on to the still younger individuals which they attend, or sometimes they eat it themselves. In the Common Gallinule or Moorhen, this appears to have become a ritual (see Annotated List, p. 209). I have seen helpers take food from their parents in the Southern House Wren, and Brackbill has witnessed the same in the Cardinal. Probably many young birds only a month or two old have difficulty in finding more food than is needed to satisfy their own hunger. In captivity, where an abundance of food is spread before them, they may indulge as freely as they like in the adult activity of feeding helpless young without stinting themselves. Hence a large share of the records of young helpers refer to captive or semi-captive birds, who fed young of their own or of other species that were closely associated with them in the aviary. Among the more interesting instances are those of the Purple Martin and the Eastern Bluebird recorded later in this paper.

Even nestlings may pass food to their nest mates, as has been recorded for the European Cormorant, the American Flamingo, the Crowned Hornbill, and a hybrid dove only 12 days old (Nice, 1943:79). A captive Chipping Sparrow about 39 days old fed a still younger Redwinged Blackbird. All of these extremely precocious birds evidently had superabundant food supplied to them by their parents or human attendants. Apparently not until they are somewhat older and more self-sufficient do birds offer to others food for which they have themselves foraged. A Golden-masked Tanager was first seen to do so when 46 days old, a Smooth-billed Ani when 48 days old, and a Southern House Wren when 54 days old.

Innubile intraspecific helpers.—Although the distinction between innubile and adult individuals is clear and the ascription of helpers to the correct category is indispensable for the full understanding of the behavior that now occupies our attention, in practice it is frequently difficult to decide with which class of helpers we are dealing. Often we cannot tell whether a nonbreeding bird is innubile or mature unless it has been banded as a nestling or fledgling and its history followed for several years. Whenever one sex far outnumbered the other and the helpers are all of this more numerous sex, as in the Black-eared Bushtit, the Pygmy Nuthatch, and the Brown-headed Nuthatch, there is a strong suspicion that they are mature individuals who lack nests of their own because mates are not available to them. Because of this practical difficulty, in my earlier paper (1935) I lumped together, under the heading of "unmated helpers," innubile helpers and mature helpers who lacked mates.

My conclusion (1935:265) that the helpers in the Brown Jay are sexually immature or inactive yearlings has recently been confirmed by Selander (1959:394). Probably the helpers in the White-throated Magpie-Jay are also innubiles. It is likely that at least some of the helpers at the nests of the Blue Fairy Wren, and of related species, belong to this class; for at some nests Rowley found, in addition to the parents, attendants of both sexes which were one year or more old and were in full breeding plumage. If these helpers were sexually mature, as their plumage suggested, why should a male and female be attending the nest of another pair instead of mating with each other and rearing their own brood? I am also inclined to include among the innubile helpers those of the Collared Araçari and the Banded-backed Wren, and at least some of the Chimney Swifts that assisted mated pairs.

To judge by my experience with the Brown Jays, innubile helpers are likely to be found at the majority of the nests of those species in which they are present, whereas most other classes of helpers are of more sporadic occurrence. The conditions which favor the occurrence of innubile helpers are not only the postponement of reproductive maturity until the second nesting season following hatching or even later, which is found in many species, but likewise a higher degree of sociability in the breeding season and more tolerance of extra individuals at the nest than most birds exhibit. Since innubile individuals have long been full grown and are well able to take care of themselves, they are likely to become efficient helpers; and they may be even more zealous in the defense of the nest and young than are the parents, as I found in Brown Jays.

Nonbreeding adult intraspecific helpers.—The best examples of this class are four species in which males are substantially more numerous than females: Arctic Tern, Black-eared Bushtit, Pygmy Nuthatch, and Brown-headed Nuthatch. In at least the three last-mentioned species, male helpers were found at a number of nests but no female helpers were noticed, which points strongly to the conclusion that the males had remained unmated because no partners were available. In the Golden-masked Tanager, in which the sexes are often indistinguishable by plumage, a third individual in adult plumage is found at such a small proportion of the nests that one can hardly surmise the helper's status; possibly it is an individual that cannot find a mate, but it is equally probable that it is a breeding bird that has lost its mate and offspring. The same difficulty of interpretation applies to all those species, including the Wheatear, Kentucky Warbler, Blue Dacnis, and Speckled Tanager, for which there is a single record of a helper in adult plumage. Possibly some of these helpers are individuals suffering from some physiological derangement that prevents breeding.

Breeding unilateral intraspecific helpers.—Unilateral helpers attend the eggs or young of other parents who do not reciprocate. The services which these unrequited breeding helpers render to the offspring of other parents of their own kind are usually occasional or sporadic rather than sustained, although at times lost or orphaned young may be adopted and reared until they become self-supporting. Kentish Plovers and Avocets sometimes brood their neighbors' chicks; although this kind office may be reciprocated, probably more often it is not. A female Purple Martin fed the hungry young in a neighboring nest from which the female parent had been carried off for a homing experiment. Adoption of strayed or orphaned young of their own kind has been reported for European Blackbirds (*Turdus merula*), American Robins, Winter Wrens, and Great Tits; occasional feeding has been observed in the Wood Thrush, Scarlet-rumped Black Tanager, and Rose-breasted Grosbeak. Most inconsistent was the behavior of a breeding Buff-throated Saltator that tried hard to drive away another female whose nest had been built unusually close to her own. The eviction of the more timid female would have

been fatal to the newly hatched nestling of that female, whereas the destruction of this nestling would have hastened the departure of the timid female. Yet the dominant female sometimes fed this nestling—a most convincing demonstration of the strength of a parent bird's impulse to feed.

Parents whose young have just been lost continue to bring food to the vicinity of their nest, and if responsive young of other families are close by, they may become the beneficiaries of the thwarted parental impulses. This has been reported for terns of several species, for Murres, and for Tree Swallows. The helpers that are often found at nests of the Long-tailed Tit may be breeding birds whose nests have been destroyed too late in the season for renesting.

Mutual intraspecific helpers.—Mutual helpers are necessarily breeding individuals. They are on rare occasions found in species which normally rear their broods alone: two Wood Ducks incubated in the same box; two pairs of Cardinals shared the same nest, as did two pairs of Song Sparrows. In a few species, cooperation among breeding pairs has become a frequent, if not an invariable, habit. Among these we may include all those which build bulky nests containing a number of compartments, such as the Gray-breasted Parakeet of southern South America, the Social Weaver of South Africa, the Palm-Chat of Hispaniola, and possibly the Rufous-fronted Thornbird of tropical South America. The construction of the framework of these avian apartment houses is certainly a community project, although each pair may finish its own chamber and rear its family without help from its neighbors. Even more complete cooperation is not improbable in these gregarious birds, of which, unfortunately, we lack detailed studies.

The best known examples of complete mutual helpfulness are the anis (*Crotophaga*), in which the several cooperating pairs share the labors of the nest at every stage of building, incubating, and rearing the young. Fragmentary observations suggest that equally close cooperation may occur among breeding pairs of certain barbets and helmet shrikes. Under this heading we may also include those megapodes in which a number of pairs construct the mound in which the eggs are incubated by the heat generated by fermenting vegetable tissues. These mound builders pay no attention to the exceptionally precocious young.

Immature interspecific helpers.—Although wild immature birds not infrequently attend younger individuals of their own kind, the only instances of immatures helping members of other species that have come to my notice refer to birds in aviaries. Well fed captive young, only a month or two old, often give food to the nestlings or fledglings closely associated with them in the same compartment. One of the most remarkable of these young helpers was an Eastern Bluebird, only six weeks old, which helped to nourish 15 nestlings of half a dozen kinds. A captive young Black-shouldered Kite, after rearing to independence nestlings of her own species, adopted a day-old buzzard chick and fed it until it was three times her own size.

Nonbreeding adult interspecific helpers.—No case of an innubile interspecific helper has come to my attention, and even nonbreeding mature interspecific helpers appear rarely to have been recognized. A wild male Canada Goose that guarded a brood of ducklings provides one of our few examples of this behavior. An old, unmated Wood Thrush, which in an aviary helped to feed 15 nestlings of various kinds, seems likewise to fall under this heading.

Breeding unilateral interspecific helpers.—A nonreciprocal relationship between breeding birds of distinct species is the form of helpfulness that has been most frequently reported by bird watchers everywhere. In addition to the numerous cases of helpers definitely known to be breeding, it is probable that most of the birds of un-

known status that were found feeding the young of some other species were, or recently had been, engaged in reproduction. Although usually passerines are discovered attending other passerines, the helpers and the helped sometimes represent different orders. The combinations are so diverse that one suspects that each species of altricial bird has occasionally helped every other altricial species of about the same size with which it has been associated over a wide area for many generations. Unlike some of the examples of intraspecific helpers that we have noticed, these instances of interspecific aid are too sporadic to be of importance in the economy of any species, but they give us fascinating glimpses into the psychology of birds.

Sometimes the helper is a male whose mate is incubating, as has been reported for the Eastern Bluebird, Winter Wren, Carolina Wren, Scarlet Tanager, and Oregon Junco. Such males are often so impatient to begin feeding their nestlings that they offer food to the unhatched eggs. This latter behavior I have called "anticipatory food bringing" (Skutch, 1953a). The feeding of a neighbor's offspring may provide an outlet for repressed energy; and in all territorial birds, the nearest nests are more likely to belong to some other species than to other individuals of the same species.

In other cases, the helpers have lost their own nestlings, or they have reared their fledglings to independence without exhausting their impulse to feed or otherwise attend young birds. Among these may be mentioned the Mourning Dove that mothered nestling White-winged Doves (*Zenaida asiatica*), the Eastern Phoebe that fed Tree Swallows, the European Blackbird that offered food to any bird who came near, the European Robins that fed nestling Song Thrushes (*Turdus ericetorum*), the male Cardinal that fed fledgling American Robins, and the Brown Towhee that nourished fledgling Cardinals. Sometimes a parent bird gives food to young not its own because its intention to feed its own offspring is temporarily thwarted, as in the case of the female American Redstart which, when her own young were held by children to be photographed, gave her billful of food to American Robins in a neighboring nest. At other times, a parent bringing food to its offspring may fly past other young birds, whose gaping mouths appeal irresistibly to parental instincts, as in the case of the Gray Wagtail that fed thrushes. The calls of a neighbor's nestlings may be similarly impelling, as in the case of the European Nuthatch that often took food to young Starlings (*Sturnus vulgaris*) in a hole three feet distant from its own nest.

More surprising are the instances of breeding birds that neglect their own nests to attend those of other species. Among these we may mention the female Tropical Gnatcatcher that became so engrossed in caring for a brood of Golden-masked Tanagers that she ignored the nest which her mate was building a few feet away, and the Blue Tits that abandoned their own eggs in order to feed European Robins in a nest built on the roof of their box.

Sometimes parent birds become helpers by accident, as appears to be true of a pair of Mountain Chickadees. Their nest in a rotting pine trunk had been separated from a hole of Williamson Sapsuckers (*Sphyrapicus thyroideus*) by a thin partition which collapsed, dropping their nest down into the sapsuckers' chamber. Thereupon, the chickadees began to feed the young woodpeckers.

The relations between the helpers and the parents of the young which they attend are various. Sometimes the helper is belligerent toward the parents, as in the case of the male Oregon Junco that fed nestling Bewick Wrens (*Thryomanes bewickii*) and the Tropical Gnatcatcher that attended a Golden-masked Tanagers' nest. More often, the parents are troubled by the presence of the uninvited assistant, and they may try to drive it away. Examples of this are the Mourning Dove at the White-winged Doves'

nest, the Eastern Phoebe at the Tree Swallows' nest, the Black-and-White Warbler at the Worm-eating Warblers' nest, and the Eastern Bluebird at the Northern House Wrens' nest. In other instances, the parents and helpers work together in concord, as happened when a Worm-eating Warbler fed nestling Ovenbirds (*Seiurus aurocapillus*), when a male Cardinal attended fledgling American Robins, and when a Brown Towhee attended fledgling Cardinals. Rarely the parents take food directly from the helper and either pass it to their nestlings or eat it themselves; Black-headed Grosbeaks accepted food from a Northern House Wren, and Yellow Warblers (*Dendroica petechia*) from Song Sparrows.

The same contrasts in the attitude of the parent birds to their assistants, and of the latter toward the parent birds, are found in intraspecific associations, and they suggest the two distinct routes by which birds are led to attend the nests of other individuals. In some species, prolonged close association between the parent birds and their offspring brings the latter into intimate contact with subsequent broods of the parent birds, in the same breeding season or, in the case of birds which pass through an innubile stage, in some following year. Most immature and innubile intraspecific helpers, and even some mature intraspecific helpers, are led in this way to assist at others' nests. In these cases, it is difficult to decide whether the nonbreeding birds are stimulated to engage in parental activities by seeing the parent birds do so or by the direct appeal of eggs or nestlings to their latent parental impulses.

The other route is that followed by most interspecific helpers and even some intraspecific helpers; these birds are not closely associated with the parent birds until accidental contact with their nest or young, at a time when they are particularly susceptible, releases parental activity, in the course of which they come into close contact with the parents themselves. The attitude toward each other of the birds thus suddenly brought together may be either friendly, hostile, or indifferent. In the first group of helpers, the social bond is primary and participation in parental offices arises secondarily from it. In the second group of helpers, the appeal to parental impulses is primary and mutual accord may in some instances develop from it, as when parents and helpers cooperate amicably in the care of the nestlings, the former sometimes even accepting food directly from their assistants. In other cases, however, participation in a common endeavor fails to overcome the antagonism between the parents and the intruding collaborators.

Mutual interspecific helpers.—These most curious cases of mutual helpfulness arise when two birds of distinct species build their nests close together or even lay in the same nest. A Rufous-sided Towhee and a Field Sparrow had nests only 18 inches apart in the same tree, and both nests contained nestlings of about the same age. The male towhee frequently fed the young sparrows and removed their droppings, and a parent sparrow likewise brought food to the nestling towhees. More often, the mutual helpers lay eggs in the same nest, and the parents of both species incubate alternately or even together, sitting side by side, or perhaps one upon the other. When successful in hatching out the mixed family, they may cooperate in brooding and feeding the nestlings. These disparate nesting partners have consisted of a Mourning Dove and a Yellow-billed Cuckoo, a Mourning Dove and an American Robin, a European Robin and a Willow Warbler (*Phylloscopus trochilus*), a European Robin and Pied Wagtails (*Motacilla alba*), a Cardinal and a Song Sparrow, and House Finches and American Robins.

Unless the nestlings of the two cooperating species hatch at about the same time, are of approximately equal size, and have similar food requirements, it is unlikely that both kinds will be successfully reared. The mixed brood of Mourning Doves and American Robins survived until they were eight days old, and I suspect that the very different

feeding responses of doves and thrushes insured that each nestling received nourishment only from its own parents. In the joint nesting of Cardinals and Song Sparrows, only the young of the larger Cardinal were fledged. When House Finches and American Robins nested together, the nestling robins smothered their smaller nest mates. But when European Robins shared a nest with Pied Wagtails, the nestlings of both species appear to have been successfully reared. No mutual partnership of this sort has proved sufficiently profitable to give rise to habitual symbiotic nesting by two species, corresponding to the intraspecific communal nesting of the anis. The fostering of the young of parasitic cuckoos, honeyguides, and cowbirds by a wide variety of other species is a wholly unilateral relationship. As in the numerous instances of birds hatching the eggs of other nonparasitic species occasionally deposited in their nests, such unintentional service to other birds falls beyond the scope of this paper. Helpers do more than incubate the eggs which some other bird has dropped into their nest, and which perhaps they do not distinguish from their own; in one way or another, they deviate from the typical breeding pattern in order to serve, or enter into close association with, individuals other than their own mate and offspring.

Intraspecific helpers not associated with reproduction.—To this group belong adult birds, unable to forage for themselves, which have remained alive and well and which have been sustained by food supplied by their companions. Recorded instances of this sort are not numerous. One of the most celebrated is that of a blind American White Pelican, alive and well in a breeding colony of its kind. Since its condition made fishing impossible, it was obviously nourished by its neighbors. Similar care of crippled or incapacitated individuals has been reported for an adult Brown Booby with only one wing, an adult Magnificent Frigate Bird in the same plight, blind Indian crows, a wounded crow attended by its companions in a hollow tree, and an adult male Black-headed Grosbeak with a deformed bill that evidently made foraging difficult. In captivity, a male European Robin fed a rival after the latter broke his leg.

Once I saw, in a band of Fiery-billed Araçaris (*Pteroglossus frantzii*) an adult, in apparently good condition, whose bill was so grotesquely deformed that it seemed impossible that it could feed itself. Apparently it depended on offerings from its companions to sustain its life. This is not improbable, since adult araçaris have been seen to feed each other (Skutch, 1958:209). But we must not too hastily conclude that because a bird's bill is misshapen it cannot forage. A Common or Bronzed Grackle (*Quiscalus quiscula*), whose upper mandible was about twice as long as the lower and otherwise malformed, managed by its own efforts to thrive for at least two years, despite this severe handicap (Bent, 1958:412).

Apparently the helpless birds I have just mentioned persuaded their companions to feed them by begging in the manner of fledglings. In species in which the male passes food to his mate, an intensification of this usual behavior, stimulated by the more persistent pleading of the hungry, helpless partner, might suffice to keep the latter alive. In the case of the Black-headed Grosbeak with a deformed bill, the female seems to have assumed the role that normally belongs to the male. Yet even in normal birds without visible defect, one occasionally notices such a reversal of nuptial feeding; I have seen it in the White-flanked Antwren (*Myrmotherula axillaris*) and in the Tawny-bellied Euphonia (*Tanagra imitans*).

Interspecific helpers not associated with reproduction.—A Raven that passed food through the bars of its cage to a free Black Vulture is my only example of this class in which both of the participants were birds. Nuptial feeding is common in the Corvidae, and possibly the well-fed captive Raven was treating the other big black bird as its

mate. But what shall we say of the free Cardinal which fed goldfish? Had this bird lost its nestlings or fledglings, and did the open mouths of the fish provide a stimulus for feeding? The motive of this Cardinal was evidently quite different from that of the Green Heron (*Butorides virescens*) that gave bread to fish in order to spear them when they approached to nibble at it (Lovell, 1958).

Helpers and the rate of reproduction.—In view of the widespread tendency of immature birds to engage in parental occupations, one may well ask why natural selection has not seized upon and elaborated this habit to increase the reproductive potential of those species in which maturity is delayed for several years, or even of more rapidly maturing species which rear two or three broods in a season. Parents with two or more yearling helpers should be able to rear twice as many young as unaided parents of the same kind; hence strains with helpers should increase more rapidly than those which lack them, finally supplanting the latter. Yet helpers are exceptional even among species which do not begin to breed until two or more years of age; and no species that I know lays more eggs than one would expect from its systematic position and environment because of the fact that helpers are available. Brown Jays, for example, lay two or three eggs in a set, although four, five, or even seven grown birds may attend the nestlings.

The answer to the foregoing question seems to be that if a higher rate of reproduction were advantageous to a species, putting the immature individuals to work at the nests of mated pairs would not be the most efficient method of achieving it. The more bustle and activity there is at a nest, the more likely it is to draw the attention of predators. In the tropical forest, where breeding birds have more enemies than in many other environments, nests rarely contain more than two eggs or young, and the parents as a rule bring large but infrequent meals, thereby minimizing the likelihood of directing hostile eyes to the nest. Helpers seem to be most frequent among birds whose eggs and young are somewhat inaccessible, as in the enclosed nests of Banded-backed Wrens and bushtits, or in those species whose size and strength enable them to repel at least the less powerful predators, as in jays. Yet even nests of the large and aggressive Brown Jays are by no means immune to predation.

If an accelerated rate of reproduction were highly advantageous to any species whose young mature slowly, it appears that this could be more efficiently achieved by hastening the advent of the adult state than by making helpers of the innubiles. Being more efficient, the former is the course which natural selection should favor. Why birds which have long been fully grown should pass from one to six breeding seasons without themselves reproducing, certainly poses a problem to one who reflects that the mammals with which we are most familiar are ready to beget offspring even before they have attained adult size. It would seem to require relatively slight physiological adjustments to advance by one or several years the attainment of reproductive maturity by all those penguins, albatrosses, fulmars, gulls, terns, swifts, crows, jays, and others which now pass one or more breeding seasons as innubiles. The existence of this large nonbreeding class is impressive testimony that its members are not needed as breeders; that, in fact, it would be disadvantageous to the species to have them engage in reproduction. The presence of helpers, and especially of innubile helpers, is, then, one more link in the lengthening chain of evidence pointing to the conclusion that birds have a considerable store of unused reproductive potential and that their reproductive rate has, in many cases, been delicately adjusted to the conditions of their lives rather than pushed to the limit of their power to rear offspring, as some have contended (Skutch, 1949; 1953c).

AN ANNOTATED LIST OF HELPERS

Pelecanus erythrorhynchus. White Pelican. An old, blind pelican was found alive in a breeding colony. Since it could not feed itself, it must have been fed by its neighbors (Baird and Stansbury, 1852:193; frequently quoted by other authors).

Sula leucogaster. Brown Booby. An adult that had lost a wing was kept alive by the food which its neighbors in a breeding colony supplied to it (Murphy, 1936).

Phalacrocorax carbo. Great or European Cormorant. Nestling cormorants sometimes feed each other, and they help to work loose material into the nest (Kortlandt in Armstrong, 1947:192; Nice, 1943:79).

Fregata magnificens. Magnificent Frigate Bird. An adult lacking a wing was supplied with food by its neighbors in a breeding colony (Murphy, 1936).

Phoenicopterus ruber. American Flamingo. Young flamingos feed each other (Chapman in Armstrong, 1947:192).

Branta canadensis. Canada Goose. A wild male goose accompanied and guarded a brood of 13 (domestic?) ducklings, along with the female duck, who "seemed to welcome the gander." He followed the family in the rear and stayed with them all day (Messenger, 1949).

Aix sponsa. Wood Duck. Two females laid in the same nest box and incubated side by side. For several days, each had her own position in the box; but later they shifted about, showing no attachment to any particular part of the box or cluster of eggs (Bellrose, 1943).

Melanitta deglandi. White-winged Scoter. "In all species of ducks, one parentless brood may on occasion join another in its entirety, and the process may repeat itself until finally a large aggregation results. An extreme case is that of a white-winged scoter that I saw with eighty-four young, all under two weeks of age! Lesser scaups [*Aythya affinis*] are commonly seen with broods of twenty or more, sometimes with two or more hens attending such combined families" (Hochbaum, 1960:56).

Elanus caeruleus. Black-shouldered Kite. A captive fledgling fed and brooded nestlings of her own kind, rearing them from the age of one day to independence. She also adopted a day-old buzzard, which she continued to feed for nearly two months, until it was three times her own size. She "brooded" a red notebook and other inanimate objects of the same color (van Someren, 1956:68-69).

Megapodius freycinet. Scrub Fowl. A mound, in which the eggs are incubated by heat generated by the fermentation of a great mass of vegetation kicked together by the birds, is sometimes attended by several pairs (Frith, 1956:633).

Gallinula chloropus. Common or Florida Gallinule, Moorhen. On a weedy pond near Cartago in the Costa Rican highlands, I found, on July 1, 1952, a family consisting of two adults, two full-grown young birds in grayish plumage with dark bills and foreheads, and four downy chicks, which kept up a constant peeping. The full-grown young birds seemed to give as much attention to them as the parents did, and once one of the former appeared to pass food to a downy chick. The feeding of younger siblings by gallinules has also been reported by McIlhenny (Nice, 1943:79) and for the British form by Finn (Armstrong, 1947:192) and by Grey (1927:155-157). Grey watched the parents give pieces of bread to full-grown young hatched in May, who then passed this food to the downy chicks born in July. When a parent gave bread directly to a chick, one of the older young took it from the downy one's bill and then replaced it there.

Fulica atra. European Coot. The feeding by immatures of still younger birds has been reported by Ruthke (Nice, 1943:79).

Laterallus leucopyrrhus. Rail. In captivity, young individuals fed younger siblings (Meise in Nice, 1943:79).

Charadrius alexandrinus. Snowy or Kentish Plover. Some birds of both sexes take an interest in chicks of other birds, of their own and related species and may even brood them (Walters, 1959).

Recurvirostra avosetta. European Avocet. Parents brood recently hatched chicks of their neighbors (Selous, 1927:223-224).

Sterna paradisaea. Arctic Tern. Some of the younger males, unable to breed because of a shortage of females, attached themselves to nesting pairs and helped to feed the chicks (Cullen, 1957). In time of scarcity, when mortality among young is high, terns of various species feed chicks belonging to other individuals (Palmer in Armstrong, 1947:190).

Uria aalge. Common Murre or Guillemot. Bereaved adults, and even those with chicks, brood

and feed others' chicks; but the parents of the latter resent neighbors' attentions to their young. Parents that have lost chicks also "feed" imaginary ones (Perry, 1946:174-200).

Columba livia. Rock Dove or Domestic Pigeon. A fledgling about 25 days old regurgitated food to a younger companion. Another young pigeon, about a month old, took sticks to the nest where its mateless mother incubated and presented them to her as an adult male does to his mate. After some initial difficulties, it daily incubated its mother's eggs for about two hours at a stretch (Goodwin, 1947).

Zenaidura macroura. Mourning Dove. One of these doves brooded and fed nestling White-winged Doves (*Zenaida asiatica*) a few days old, which had been neglected through most of the day by their own parents. When at last the female White-winged Dove returned in the late afternoon, she fought and drove away the fostering Mourning Dove. The latter, however, continued to minister to the young White-wings until they fledged. Apparently her own eggs had failed to hatch. In aviaries, Mourning Doves and several other kinds of doves are quick to adopt and assist in the care of young doves of any species (Neff, 1945). See also Yellow-billed Cuckoo and American Robin.

Myiopsitta monachus. Gray-breasted Parakeet. Many pairs unite to build a huge arboreal structure of interwoven thorny twigs. This communal nest may weigh a quarter of a ton; it contains many chambers, apparently each the nest of a single pair (Hudson, 1920, 2:30-33).

Coccyzus americanus. Yellow-billed Cuckoo. This species and the Black-billed Cuckoo (*C. erythrophthalmus*) often lay eggs in each other's nests, as likewise in the nests of a number of other small birds, possibly because their own poorly built structures have capsized while their eggs were ready for deposition. On one occasion, a Yellow-billed Cuckoo laid two eggs in a nest of the American Robin (*Turdus migratorius*), in which the robin also laid an egg. Then a Mourning Dove added two eggs to the mixed set and incubated along with the cuckoo. Both birds were found sitting side by side on the eggs of three kinds (Bent, 1940:56).

Crotophaga sulcirostris. Groove-billed Ani. Although about half the nests belong to single pairs, two, three, or rarely more pairs may join in building a communal nest, in which all the females lay their eggs in a single mass. All the cooperating parents take turns at incubating and brooding, one at a time, and a single male takes charge of the nest through the night. All the parents feed the nestlings, without distinguishing their own. Beginning at the age of 72 days, a young ani of the first brood fed and defended nestlings of its parents' second brood (Skutch, 1959).

Crotophaga ani. Smooth-billed Ani. In its communal nesting arrangements, this species resembles the Groove-billed Ani, but the cooperating group may be larger, containing up to five females in some instances. At the age of 48 days, a young bird of the first brood fed nestlings of the second brood (Davis, 1940). When about six weeks old, a hand-reared ani carried and arranged sticks and straws (Merritt, 1951:229).

Crotophaga major. Greater Ani. This large ani nests communally, like the smaller species (Davis, 1942).

Guira guira. Guira Cuckoo. Pairs may nest alone, or several may attend a communal nest, as in the anis (Davis, 1942).

Caprimulgus europaeus. Nightjar. An extra adult helped to feed nearly grown young (Stülken and Brüll, 1938).

Chaetura pelagica. Chimney Swift. Extra birds frequently assist parents in incubation, brooding, and feeding the nestlings. Some nests have two of these helpers simultaneously, in addition to the two parents. The assistants are of both sexes but more often males than females. Some are yearlings, others old birds apparently in their last year of life; but some are of intermediate age and engage in active reproduction in later years. The helpers roost clinging to the wall of the chimney or air shaft near the nest, in company with the parent or parents who are not incubating or brooding. Sometimes they roost with the fledglings (Dexter, 1952; Sherman, 1952:47, 56).

Lophoceros melanoleucos. Crowned Hornbill. After the emergence of the female from the nest cavity in which she is sealed from the start of laying until the nestlings are half grown, the young birds, working from within the hole, plaster up the doorway again, leaving a gap just wide enough for the parents to pass food to them. Captive nestlings placed in a box with a small opening proceeded to reduce its size with mud supplied to them, with particles of food, and with their own drop-

pings. They attended efficiently to the sanitation of their box. One of them proffered food to its nest mates (Moreau and Moreau, 1940:641-644; Moreau, 1936:25-26).

Lophoceros deckeni. Red-and-White-billed Hornbill. After the emergence of the mother from a nest hole, two nestlings, 21 to 25 days old, replaced the plaster seal with material they found inside the hole (Moreau, 1936:22-24).

Bycanistes subcylindricus. Casqued Hornbill. On several occasions, intruding individuals offered food to a female of the same species who was enclosed in her nest hole in a tree. When the mate of the enclosed female returned, he chased the trespassers away (Kilham, 1956:26-27).

Buccanodon leucotis. White-eared Barbet. In tropical Africa, four adults brought food to a hole containing four nestlings. Since other nests of this species contained only two or three eggs, this is, apparently, an instance of communal nesting (Moreau and Moreau, 1937:171-172).

Lybius albicauda. Pied Barbet. In addition to the parents, two birds occasionally brought food to nestlings (van Someren, 1956:209-212).

Pteroglossus torquatus. Collared Araçari. Early in the year, six grown individuals of this small toucan slept in a high, inaccessible hole in a tree in the Panamanian forest. After eggs were laid in this hole, a single individual passed the night in it. Later, when the eggs hatched, there were, in addition to the nestlings, five lodgers, all of whom brought food to the young, of which there were at least three. These attendants probably consisted of the two parents and three innubile helpers (Skutch, 1958:201-207).

Tripus chrysaucaen. Golden-naped Woodpecker. As I described in an earlier paper (1948), fledglings return to sleep with their parents in the hole in which they were reared. The entire family may continue to lodge together in this hole, or in others built to replace it, until the following breeding season, when the parents move into a newly finished hole and the young of the preceding year depart. In El General, this woodpecker usually rears a single brood; but in 1960, after an exceptionally early first nesting, a pair undertook to raise a second brood in a neighboring hole. The three young females of the first brood slept with the two parents in the nest cavity while the eggs of this later brood were being incubated and the nestlings were growing up. Apparently the young birds did not help their parents to incubate the eggs with which they were thus closely associated, but after the eggs hatched, they sometimes entered the hole with the nestlings by day and probably brooded them. This seemed at first to upset the parents, and the adult female was mildly antagonistic toward the young females when they approached the nest. After the nestlings began to look through the doorway, at least two of the young females, then in their fourth month, brought small particles of food. But they seemed to fear the grasping thrust with which older nestlings take their meals. Instead of delivering their offerings from the outside with head turned sideways to facilitate its transfer, as the parents did, after considerable hesitation the young females pushed quickly through the doorway with their heads bent down to avoid the nestlings' bills. Since all the food which the young woodpeckers brought was taken inside, I could not learn how much of it the nestlings actually received. It was evident, however, that the parental behavior of these helpers was imperfectly developed. They brought to feathered nestlings particles of the size that should be given to newly hatched ones, and they did not present this food in the proper manner.

After two young of this second brood were fledged, the hole in which they were reared was entered each evening by seven woodpeckers, including the two parents, three females of the first brood, and a male and a female of the second brood. Soon the stub that contained this hole fell, and the parents proceeded to carve a new dormitory. At least one female of the first brood helped in this work; and even the male of the second brood, now about 57 days old, three weeks out of the nest, and still receiving occasional meals from his parents, took part in the undertaking. I could not see how much carving he did inside the cavity, but one morning he threw out ten billfuls of chips in about half an hour. Each billful was smaller than those which adults customarily remove while carving.

In its family life, the Golden-naped Woodpecker stands between species of *Centurus*, whose habits I briefly outlined in an earlier paper (1943), and the following species.

Balanosphyra formicivora. Acorn Woodpecker. Leach (1925) reported that in California a whole flock of these woodpeckers participates in a nesting. Apparently more than two individuals help to carve the nest hole and take turns incubating the eggs. At least five, and possibly more, brought food to a single brood of nestlings. In Costa Rica, this woodpecker has similar customs. In an inaccessible

nest, four males and one female were taking turns at incubation and changing over very frequently. At another nest, at least two males and one female were incubating. At yet another nest, at least two males and two females were bringing food to an undetermined number of well-grown nestlings (Skutch, 1943, and later observations). Unfortunately, neither Leach nor I was able to learn the contents of the nests that we watched. Without this information, we cannot decide whether several pairs nest communally, as in anis, or a single breeding pair is assisted by helpers.

Phacellodomus rufifrons. Rufous-fronted Thornbird. In Venezuela, four birds were seen working on a bulky nest of interwoven sticks that had three entrances, apparently giving access to separate chambers (Gilliard, 1959:19-20).

Sayornis phoebe. Eastern Phoebe. A female whose first brood was becoming independent brought food to nestling Tree Swallows, continuing this for about a week, while the parent swallows tried to drive her away (Deck, 1945).

Progne subis. Purple Martin. At the age of 54 days, a hand-reared female tried to brood nestlings and soon began to bring insects to them (Richmond, 1953:245-246). When a female parent was carried away for a homing experiment, the mother of a brood in an adjoining compartment in the bird house fed the absent mother's nestlings as well as her own. The mate of the absent female accepted this assistance without protest (Southern, 1959).

Delichon urbica. House Martin. As many as 14 martins may cooperate in building a single nest. Four or more individuals often feed a single brood. Some of these attendants are the young of earlier broods (Bent, 1942:435-436; Witherby *et al.*, 1938, 2:236).

Petrochelidon pyrrhonota. Cliff Swallow. Three individuals sometimes build together and take turns incubating the eggs (Bent, 1942:474).

Hirundo rustica. Barn Swallow. In both Europe and North America, young swallows appear not infrequently to feed the nestlings of their parents' subsequent brood. Sometimes they may even help to build the nest for this brood; in one instance they engaged in this work about a week after they took wing. Occasionally a third adult helps to feed the nestlings (Nice, 1943:79, 243; Armstrong, 1947:191-192).

Riparia riparia. Bank Swallow or Sand Martin. The excavation of burrows is a communal activity, the climax of an elaborate aerial display, in which many swallows participate. The number of holes is at first approximately the same as the number of individuals present. At one display, from three to six birds may be active at a single burrow, while at the next display, excavation is carried on at quite different holes. The same swallow may move from hole to hole, digging at several in succession (Hickling, 1959).

Iridoprocne bicolor. Tree Swallow. More than two attendants at a nest are not uncommon. The nestlings in one box were attended by four to six adults, of which at least three were males and at least one a female. In another locality, at least three broods had an extra attendant, a female whose own young had died (Bent, 1942:387).

Tachycineta thalassina. Violet-green Swallow. Sometimes two or even three females bring food to the young in a single nest (Shirling in Bent, 1942:378-379).

Corvus corax. Common Raven. In freezing weather, a captive in a zoo passed food through the bars of its cage to a free Black Vulture, *Coragyps atratus* (Davis, 1952).

Corvus monedula. Jackdaw. A captive young bird fed younger individuals (Strauss in Nice, 1943:79).

Corvus brachyrhynchos. American Crow. Three crows were watched building one nest in Boston, and three were seen feeding the young in one nest in Connecticut. Nests containing two sets of eggs have been reported (Forbush, 1927:395).

Corvus sp. "Indian crow." "Mr. Blyth, as he informs me, saw Indian crows feeding two or three of their companions which were blind; and I have heard of an analogous case with the domestic cock" (Darwin, 1871, ch. 4).

Corvus sp. Crow. "Brehm himself saw two crows feeding in a hollow tree a third crow which was wounded; its wound was several weeks old" (Kropotkin, 1902:59).

Psalorhinus mexicanus. Brown Jay. The bills of young birds are yellow, and they turn black gradually and irregularly, providing patterns which facilitate the recognition of individuals. Pied-billed innubiles, apparently about a year old, assist the darker-billed parents in the duties of the nest,

sometimes bringing sticks during construction or feeding the incubating female, often bringing food to the nestlings, and guarding them, at times more zealously than the parents. At a nest with eggs, at least two helpers fed the incubating female; and at four other nests with young, one, two, three, and five helpers were distinguished (Skutch, 1935; 1960:231-257).

Calocitta formosa. White-throated Magpie-Jay. An incubating female was attended by at least two, and probably more, other individuals, who fed her 47 times in 13¾ hours, keeping her so well supplied that she found it unnecessary to forage for herself (Skutch, 1953d; 1960:258-259).

Cyanocorax dickeyi. Tufted Jay. Three individuals were interested in a nest, and two of them sat side by side on the eggs for a short while (Moore, 1938:238-239).

Aphelocoma ultramarina. Mexican Jay. Two pairs sometimes breed in the same tree, and three or four birds may join in building a nest (Bent, 1946:118-123). Seven or eight individuals, including two yearlings, collaborated in building a nest (Gross, 1949:242-244).

Aphelocoma coerulescens. Scrub Jay. A nest with two young was attended by three adults, at least two of whom brooded (Grimes, 1940).

Cyanocitta cristata. Blue Jay. "Occasionally, in winter or early spring, one of these birds is seen to feed a companion. They are said to care for the aged and infirm" (Forbush, 1927:380).

Corcorax melanorhamphus. White-winged Cough. These Australian corvids live in flocks of up to 12 individuals. The whole group may join in building the nest, a very bulky structure that is repaired year after year (Mathews, 1925-1927:414-420).

Parus major. Great Tit. A male fed the nestlings of a female Great Tit whose mate had died. A pair of these tits adopted eight fledglings which were the offspring of another pair. A young bird placed food within reach of a young male of the same brood whose leg was broken (Howard, 1952:25, 31, 102).

Parus caeruleus. Blue Tit. A pair built a nest in a box, on top of which a pair of European Robins already had a nest. The female robin laid five eggs and the tit laid three. When the robin's eggs hatched, the tits covered their own eggs with feathers and fed the young robins. At first there was a little fighting, but soon the two pairs settled down to attend the nestlings in concord. After the robins were fledged, the tits laid another set of seven eggs over the original three and raised a brood (Lonsdale in Williams, 1942:246-247).

Parus bicolor. Tufted Titmouse. Parents rearing a second brood were assisted in feeding the nestlings by two other titmice, apparently young of their first brood (Wight in Laskey, 1957:142). For two weeks, a banded unmated yearling helped to feed the three nestlings of its female parent, whose mate had died and who was now paired with another male. Although its attendance was less regular than that of the nestlings' parents, it brought food at least 89 times, while the male brought food at least 120 times and the female 126. The female parent was friendly with the helper, but the male tried to drive it away (Brackbill, 1958).

Parus gambeli. Mountain Chickadee. A pair fed nestling Williamson Sapsuckers (*Sphyrapicus thyroideus*) which were also being attended by their own parents. This situation apparently resulted from the collapse of the partition which separated the holes of these two species in the same decaying pine trunk (Russell, 1947).

Aegithalos caudatus. Long-tailed Tit. There are many records of nests at which more than two individuals were in attendance. Some of these nests held unusually large sets of eggs, which had probably been laid by two females; but often the nests with extra attendants had sets of normal size. Although most often there was only one extra bird, sometimes there were two. At one nest with a set of normal size there were certainly two and possibly four helpers. Usually these assistants feed the nestlings, but sometimes they are present during incubation. It is probable that many of these helpers are breeding birds that have lost their own brood and fail to re-nest because of the shortness of the tits' breeding season. In the absence of territorial defense, they readily attach themselves to parents with young (Lack and Lack, 1958:14). At one nest the attendants were two males and one female, and all three were feeding the ten young in complete harmony (Robertson and Porter, 1952). Immatures also feed younger broods (Morbach in Nice, 1943:79).

Psaltriparus melanotis. Black-eared Bushtit. In the breeding season, males are greatly in excess of females, and those who do not find mates assist the mated couples at the nest. At times they bring downy material to the pensile pouch while incubation is in progress, but far more often they help to attend the nestlings, feeding and even brooding them. At three nests there were one, one, and three

male helpers, most of whom slept in the cozy pouch along with the parents and the four nestlings (Skutch, 1935; 1960:211-225).

Psaltirparus minimus. Common Bushtit. At some nests a third individual helps the parents to incubate and to feed and brood the nestlings (Addicott, 1938).

Sitta pygmaea. Pygmy Nuthatch. Of 36 nests in California, eight were attended by three individuals. The extra individual was invariably a male, usually a yearling but sometimes older, who was not actually mated to the female. This helper assisted in nest construction, in feeding the female while she incubated or brooded, in feeding the nestlings, and cleaning the nest. He also fed the young birds after their emergence from the nest, and at all stages of the breeding cycle he roosted in the nest with the other members of the family. In this species, parents and offspring continue to sleep together in a suitable cavity over the winter. Many of the helpers are young males who have been for many months thus closely associated with their parents. Their failure to rear families of their own is evidently caused by the paucity of females, since the sex ratio is strongly unbalanced in favor of the males. When two family groups forage together, an adult of one family sometimes feeds fledglings of the other family. Up to six individuals have been found excavating a nest cavity, which was later used by a single pair (Norris, 1958:177, 197, 240). Nine nestlings, not an abnormally large brood, were fed by four adults (Bleitz, 1951).

Sitta pusilla. Brown-headed Nuthatch. As in the Pygmy Nuthatch, there are far more males than females in this species. An unmated male sometimes assists a mated pair at all stages of the nesting, although the helper was not found sleeping in the hole with the parents when they had eggs or nestlings. A pair which lost its nest helped to feed the nestlings of a neighboring pair (Norris, 1958:178, 187, 191). Houck and Oliver (1954) studied a nest in which seven young were fed by four adults, which they believed to be two pairs.

Sitta europea. European Nuthatch. When a pair of nuthatches nested three feet away from a pair of Starlings (*Sturnus vulgaris*), one of the former often carried food into the nest box of the latter. It also removed droppings of the nestling Starlings (Powell, 1946).

Certhia brachydactyla. Garden Tree Creeper. Captive young birds fed still younger ones (the Heinroths in Nice, 1943:79).

Argya malcolmi. Large Gray Babbler. As soon as fledglings leave the nest, they join in a band and are apparently fed and protected by the band as a whole. As a rule, only the parents attend young still in the nest, but an exception was noticed at a late nest with two nestlings. Here, five adults with food in their bills were seen in the nest tree at one time, and three of them were at the nest feeding the young (Hutson, 1947:574-575).

Armstrong (1947:191-192) mentions several other species of babblers in which small bands cooperate in building the nest or attending young, but details are not available to me. In the Jungle Babbler or "Seven Sisters" (? *Turdoides striatus*) six adults fed three young in a nest (Lowther, 1951).

Campylorhynchus zonatus. Banded-backed Wren. In the nonbreeding season, these large wrens live in family groups, which lodge in bulky covered nests, sometimes as many as 11 occupying the same dormitory. In the following breeding season, some of these birds remain with the mated pair and help them to attend the nest. At a nest with three nestlings, there was a single helper; at another nest, with five young, there were certainly two and possibly five attendants bringing food, in addition to the two parents. The status of the helpers is not known, but apparently they are innubile yearlings (Skutch, 1935; 1960:186-201).

Thryothorus ludovicianus. Carolina Wren. A male whose mate was incubating in a nest box fed not only her but likewise young Great Crested Flycatchers (*Myiarchus crinitus*) in a neighboring box (Wight in Laskey, 1948:118).

Troglodytes troglodytes. Winter or European Wren. A pair adopted fledglings of their own kind which had been hatched and partly reared by a pair of Great Tits. A wren fed two Spotted Flycatchers (*Muscicapa striata*) after they had left their nest which was close to that of the wren. Another wren fed nestling Great Tits while his mate incubated, continuing to do so at least four days. Winter Wrens have also been known to feed young Willow Warblers (*Phylloscopus trochilus*) and Linnets and to nourish a European Cuckoo (*Cuculus canorus*) that was attended by Hedge Sparrows, *Prunella modularis* (Armstrong, 1955:104-105, 233-234, 242). A wren fed nestling Coal Tits (*Parus ater*) that were nearly ready to leave their nest box, and twice it passed food to a parent of the tits (Betts, 1958:427-428).

Troglodytes aedon. Northern House Wren. A wren gave food to parent Black-headed Grosbeaks of both sexes while they brooded their nestlings; the grosbeaks ate some of this food and fed some to the nestlings. After the young grosbeaks left the nest, the wren fed them directly. A few days later, this wren brought food to a family of House Sparrows, *Passer domesticus* (Hills in Bent, 1948:125-126).

Troglodytes musculus. Southern House Wren. Fledglings newly emerged from the nest are, as the day ends, led by their parents to sleep in some sheltered nook, sometimes in the nest space itself. If the young continue to lodge in the nest space, the parents usually evict them about the time the following brood hatches; but sometimes they refuse to be driven away and sleep close to the nestlings. In these circumstances, they may help to feed their younger brothers and sisters. In one family, two immatures of the first brood attended nestlings of the second brood, and the single survivor of the second brood brought food to the third brood, beginning this activity at the age of 54 days. While attending the second brood, the young female of the first brood became antagonistic to her mother, who drove her away after a day of fierce fighting (Skutch, 1953b:137-140).

Dumetella carolinensis. Catbird. A brood of orphaned Cardinals was fed and mothered by a Catbird. Another Catbird fed a half-grown flicker (*Colaptes*) that had been dislodged from its nest and separated from its parents in a severe storm (Bent, 1948:328).

Turdus merula. European Blackbird. After rearing two of her own young, a female blackbird continued for two or three weeks to offer food to any bird that came near, and an adult European Robin was among those who accepted (Lack, 1953:99). On two occasions, a fledgling, that strayed rather far from its nest in the first day after leaving it, came into the territory of a neighboring pair that also had fledged young. In both cases, the male of the new pair promptly adopted the wanderer and fed it until it could care for itself; it was never seen to be fed by its own parents. Usually, however, young that beg from strange adults receive nothing. When two families have become mixed, the parents have always been seen feeding only their own young (Snow, 1958:22).

Turdus migratorius. American Robin. Fledglings that become separated from their parents are sometimes adopted by other adults (Young, 1955:339). Captive young robins fed still younger birds of other species (Favell in Nice, 1943:79). Robins sometimes share a nest with another individual, of the same or a different species. The most curious of a number of instances that have come to my attention is that of a robin and a Mourning Dove, each of whom laid two eggs in the same robin's nest. They took turns incubating, then fed and brooded the nestlings until they were eight days old. On the following day, the four nestlings died (Raney, 1939). A robin and a Catbird each built a nest in the same clump of lilacs. Both took turns at incubating the Catbird's eggs, and when the young hatched they were brooded by both the robin and the Catbird (Bent, 1948:328). See also House Finch.

Hylocichla mustelina. Wood Thrush. Nine days after her first brood left the nest, a female fed a strange young bird which with its parents had entered her territory (Brackbill, 1943:79). In an aviary, an old, unmated thrush helped to feed 15 nestlings of various species, including Wood Thrushes, Veeries (*Hylocichla fuscescens*), Bobolinks (*Dolichonyx oryzivorus*), Cardinals, and orioles. Her co-worker was the young Eastern Bluebird mentioned under that species (Ivor, 1944b).

Hylocichla ustulata. Swainson Thrush. A thrush assisted in feeding nestling American Robins, bringing food to the nest at least 12 times in four hours. The parent robins were present (Jewett in Bent, 1949:167).

Hylocichla minima. Gray-cheeked Thrush. Three adults fed the young in one nest (Wallace in Bent, 1949:205).

Sialia sialis. Eastern Bluebird. Five birds of the first brood, all less than two months old, diligently cared for the four nestlings of the second brood, beginning when the latter were three days old. These helpers also cleaned the nest (Laskey, 1939:28). Other instances of bluebirds feeding younger siblings are cited by this author and by Nice (1943:79). A six-week-old female bluebird fed young Wood Thrushes, Veeries, Bobolinks, Cardinals, orioles, and a cowbird, 15 in all, which were being hand reared in the same aviary. When slightly older, this same female helped to feed and to brood a nestful of young Eastern Bluebirds, sometimes sitting in the nest beside the female parent (Ivor, 1944b). An adult male fed nestling Northern House Wrens, upsetting their parents, until his mate hatched young wrens, when he transferred his attention to his own offspring (Forbush, 1929).

Sialia mexicana. Western Bluebird. Young birds fed the next brood of their parents (Finley, 1907).

Sialia currucoides. Mountain Bluebird. Three young birds of the first brood fed their siblings of the second brood (Mills, 1931:9).

Oenanthe oenanthe. Wheatear. In two instances, young birds of the first brood helped their parents to feed the second brood (Nicholson, 1930:306; Wynne-Edwards, 1952:378). On Baffin Island, a fully adult male, somewhat less boldly colored than the male parent, helped a mated pair to feed seven nestlings. Once the helper was mildly chased by the male parent (Sutton and Parmelee, 1954:298-299).

Phoenicurus ochrurus. Black Redstart. A second adult male, in better plumage than the father, helped to feed young and clean the nest. The parents, although not hostile, were disturbed, and "their efficiency in feeding the nestlings was impaired" (Ashby in Nice, 1943:243).

Erithacus rubecula. European Robin. Parents of fledglings sometimes feed strange fledglings, even those that differ considerably in age. Robins that had lost their own young fed a brood of nestling Song Thrushes (*Turdus ericetorum*). Other robins have fed young Song Thrushes, Blackbirds, and, in several instances, European Wrens. When two males were placed in the same aviary, they fought often, but after one broke his leg, his rival fed him (Lack, 1953:98-99, 82; Armstrong, 1947:168; 1955:233). A story told by Eckermann in his "Conversations with Goethe" has been frequently quoted. He found two newly fledged wrens and wrapped them in a handkerchief to take home, but they escaped while he was passing through a wood. Three days later, he found them in a robin's nest, being fed together with the nestling robins. Evidently the wrens, when seeking a snug lodging for the night as is their habit, found the robin's nest, entered it, and were accepted by the parent robins. "A robin and a willow warbler were found, each sitting on six eggs in a nest built by the latter species, and another pair raised a combined brood with a pair of pied wagtails [*Motacilla alba*]" (Lack, 1953:86).

Sylvia communis. Common Whitethroat. Captive young birds fed still younger ones (the Heinrichs in Nice, 1943:79).

Malurus cyaneus. Blue Fairy Wren. Of 18 breeding groups that were color-banded, 12 consisted of one male and one female only. Of the remaining six, four had a second male, one had both a second male and a second female, and one had two males and a female in addition to the mated pair. All these birds were entering their second year, if not older, and all were in full breeding plumage. At these six nests, each of the extra birds helped the parents to feed the young, both before and after they fledged. This was true even of the group with five attendants. Besides this assistance from other older birds, the young of earlier broods frequently feed their more recently fledged siblings. In this multiple-brooded species, the female, occupied with a new nest, may cease to feed the young after they have been out of the nest about ten days; and as the fledglings are still dependent, care by other attendants is important to them. Moreover, if a parent is killed, the helpers may rear the brood (Rowley, 1957).

Malurus lamberti. Variegated Fairy Wren. "This species is double-brooded, and very often the young of the first brood assist the parents in feeding those of the second" (Cayley, 1949:42). "A young male helps nearly every pair . . . to feed their young" (Armstrong, 1947:192, citing Waterhouse).

Malurus amabilis. Lovely Fairy Wren. At one nest, a male and three birds in female plumage fed the young, and all the attendants gave a distraction display simultaneously (Cayley, 1949:51, 55).

Malurus splendens. Splendid Fairy Wren. "At one nest, a single male and two females or immatures fed the young; at another, two fully plumaged males and only one female; while elsewhere there appeared to be only one bird of each sex" (Warham, 1954:138).

Poliophtila plumbea. Tropical Gnatcatcher. A female fed and brooded two nestlings of the Golden-masked Tanager and likewise cleaned the nest. As days passed, she became increasingly hostile to the parent tanagers, devoting more time to her futile attempt to keep these slightly larger birds away and less to attending the nestlings. The parents usually ignored her, unless she became very annoying, when they chased her mildly. Her attendance at the nest continued at least 12 days and was terminated only by the nestlings' departure. While the female gnatcatcher was so engaged, her mate built a nest in the same tree without her help, but she apparently failed to lay in it. He, in turn, took no interest in his neighbors, the tanagers (Skutch, 1960:49-52).

Muscicapa hypoleuca. Pied Flycatcher. "Helpers that are strangers sometimes associate with feeding pairs without being driven off" (von Haartman, 1956:464). A male was attending alone nestlings that had lost their mother. A strange female arrived and, despite mild attacks by the male, helped to bring food to the young. When strange young flycatchers, already self-supporting, rested atop an experimental nest box in which hungry nestlings called for food, but were inaccessible to their parents, the latter sometimes fed these strangers (von Haartman, 1953:157, 162).

Motacilla cinerea. Gray Wagtail. As a parent wagtail flew over a brood of young thrushes, they opened their mouths, whereupon the wagtail faltered in flight, turned, alighted, and gave all its food to them (Pike in Armstrong, 1947:61).

Motacilla capensis. Cape Wagtail. A third individual, possibly the young of an earlier brood, sometimes took a turn at incubating the eggs of a mated pair (Skead, 1954:98).

Anthus trivialis. Tree Pipit. Captive young birds fed still younger ones (the Heinroths in Nice, 1943:79).

Dulus dominicus. Palm-Chat. Bulky nests of interwoven sticks containing several chambers, each probably occupied by a breeding pair, are built by the combined exertions of a small flock (Wetmore and Swales, 1931:347-349).

Artamus maximus. Papuan Wood-Swallow. Three nestlings were fed by four or five adults (Gilliard, 1958:304).

Cracticus nigrogularis. Pied Butcherbird. An individual in immature plumage brought food to a nest which was also attended by two birds in adult plumage (Thomas, 1951).

Prionops poliocephalus. White Helmet Shrike. Several nests may be built close together, and sometimes two females lay in the same nest. The members of a small flock share incubation and feeding the young (Gilliard, 1958:298).

Prionops plumata. Spectacled Shrike. Four birds out of a flock of six brought material to a nest which the flock was building (Gilliard, 1958:299).

Eurocephalus rüppellii. White-crowned Shrike. Two or more females take turns on the eggs (Moreau and Moreau in Armstrong, 1947:192).

Melithreptes lunulatus. White-naped Honeyeater. Two pairs of adults fed one lot of young. In another instance, two obvious sets of eggs were found in one nest (Mathews, 1924:250).

Cyanerpes cyaneus. Blue Honeycreeper. On April 23, 1958, my wife saw a male in full nuptial attire give food to a fledgling Scarlet-rumped Black Tanager on the feeding shelf beside our house. For the next three days, the brilliant honeycreeper continued to attend the tanager, which was at least twice his size, giving it chiefly pieces of banana or plantain from the shelf and sometimes insects caught in the foliage. Again and again, this strange pair returned to the feeding shelf; and the honeycreeper stuffed the tanager with fruit, once passing it six billfuls of banana in rapid succession. The honeycreeper insisted on pushing his long, sharp bill well into the throat of the short-billed tanager, who seemed not to relish this method of delivering food. When sated, the young tanager would turn its head away, whereupon the honeycreeper would flit over its back from side to side, presenting the morsel alternately on the right and on the left, until the tanager flew away with its attendant following. Often the young bird pursued the honeycreeper through the neighboring trees, begging; but when the attendant started off on a high flight, the tanager, a member of a species which does not travel so high and far, did not follow. The tanager was beginning to feed itself, and it also received at least occasional food from a male of its kind, probably its parent. It seemed, however, to prefer the attentions of the more complaisant honeycreeper. No female tanager was seen to feed the fledgling.

Dacnis cayana. Blue or Turquoise Dacnis. In May, 1959, I found a nest of this honeycreeper 18 feet up in a guava tree close by my house. It was a light-colored open cup attached by its rim (not a covered structure as has been stated in print), excellently concealed by clustering foliage. While the female incubated her two white, speckled eggs, her mate sometimes fed her, and a second male, also in full nuptial attire, was sometimes nearby. After one of the eggs hatched, both males helped the female to feed the nestling. One male sometimes mildly chased the other; yet at other times they were at the nest together with food. When I made visits of inspection, both protested my intrusion along with the female, all uttering low, weak notes. Although this may have been a case of polyandry, I think it probable that the second male was a helper rather than another mate of the female. One of the males associated with her far more closely than the other.

Mniotilta varia. Black-and-White Warbler. One of these warblers repeatedly fed nestling Worm-eating Warblers, although the parents attacked him when he approached the nest. Once they tore food from his bill and themselves gave it to the young. The helper gave a distraction display when the observers visited the nest (Rea, 1945). A pair of Black-and-White Warblers fed a young Ovenbird (*Seiurus aurocapillus*) that had recently left the nest and had apparently become separated from its parents. They cared for the fosterling for several days (Kendeigh, 1945:147).

Helminthos vermivorus. Worm-eating Warbler. Over a period of at least five days, a Worm-eating Warbler fed four nestling Ovenbirds and sometimes cleaned the nest. Although the helper and the female parent were occasionally at the nest together, no hostility was noticed (Maciula, 1960).

Oporornis formosus. Kentucky Warbler. At one nest, a second male, which seemed to be abnormal, brought food to the incubating female, although occasionally he was chased by another male that sang better and seemed to be her mate (De Garis, 1936:423).

Setophaga ruticilla. American Redstart. While young redstarts were being photographed in the hands of children, the male parent brought them food, but the more timid female gave her food to young American Robins in a nest 25 feet away (Allen in Williams, 1942:246). A nest with a double set of eggs was attended by two females, while two males were in the vicinity (Wood in Bent, 1953: 665-666).

Passer domesticus. House or English Sparrow. In Kansas, a female sparrow brought food to three fledgling Eastern Kingbirds (*Tyrannus tyrannus*), whose parents were not seen. For at least a week, the sparrow continued to bring bread and other food to the flycatchers, although her head was usually caught by the closing of the wide mouth into which she placed the morsels and she had to struggle to release herself (Fitch, 1949). An almost identical episode is reported from Louisiana. In this case, also, no adult kingbird was seen to take an interest in the three fledglings that were fed by the female sparrow. At least one of the kingbirds was attended by the sparrow over a period of 10 days (Hamilton, 1952). A sparrow cooperated with a pair of Red-eyed Vireos (*Vireo olivacea*) in feeding and defending their nestlings (Bent, 1958:17).

Spermestes nigriceps. Black-headed or Rufous-backed Mannikin. Both adult and immature auxiliaries help to build the nest (Armstrong, 1947:192). "Several birds will combine and construct a sleeping nest capable of holding a number of birds . . . If more than two birds are taking part in nest building, the nest is probably temporary sleeping quarters. If in a week or so it does hold eggs, you will find that the occupants are now only two; the helpers in the nest building have gone off" (van Someren, 1956:477).

Quelea quelea. Black-faced or Red-billed Weaver. In an aviary, more than two adults may nourish the young in one nest, although this is not known to occur among birds in the wild (Morel and Bourlière, 1956:118).

Philetairus socius. Social Weaver. Under a roof constructed of small twigs and dried grasses by the flock as a whole, each pair builds its own nest chamber. Large communal nests may measure more than 25 by 15 feet at the base and about five in height; they contain 95 or more individual nests (Friedmann, 1930).

Quiscalus quiscula. Common Grackle. A female grackle fed and protected nestling Chipping Sparrows whose parents could not be found (Bent, 1958:412). This behavior is unexpected in a bird which sometimes preys on smaller birds.

Agelaius phoeniceus. Redwinged Blackbird. A female, whose young were lost two days after they left the nest, helped a neighboring female to feed her fledglings. She continued to do this for at least ten days (Strosnider, 1960).

Tangara larvata. Golden-masked Tanager. At one nest in Panamá and two in Costa Rica, a young tanager in juvenal or transitional plumage helped a mated pair to feed nestlings. One of these young birds, 46 days old, was noticed helping its parents to feed their next brood. At first it brought food as often as either of the parents, although often it came with a smaller portion. But after the novelty of this adult occupation wore off, it was far less regular in its attendance (Skutch, 1954:209-210). On three occasions, I have watched trios of adults, in full breeding plumage, attending nestlings. One of these trios was bringing food to a nest that contained one nestling and one unhatched egg, so that evidently this was not a case of two females laying in the same nest. The relationship of the helper to the parents is unknown.

Twice I have seen individuals in juvenal plumage gather material while their parents were building a nest for a later brood. On the second of these occasions, the young tanager tried to pull a long, strong fiber from an abandoned nest of a Blue Honeycreeper. When the fiber resisted, the tanager hung from it with closed wings until it finally came loose; but the bird then dropped the piece that it had tried so hard to obtain. The second young tanager of this family sat in the honeycreeper's nest and made movements such as a building bird uses to shape its structure.

Tangara chrysophrys. Speckled or Yellow-browed Tanager. In late May of 1959, a pair of these tanagers built in a poró tree near our house. The female was lame, with a right leg that hung uselessly; yet, despite this handicap, she managed to hatch a single nestling. Before this young bird left the nest, I noticed that two birds of the same species were feeding it, along with its lame mother. I could not distinguish the helper from her mate. In nine hours of watching, the lame female brought food 52 times and the other two attendants 62 times. Although sometimes all three came to the nest tree together, more often the helper was alone. After the fledgling left the nest, I repeatedly saw its three attendants carry banana from the feeding shelf.

Tangara inornata. Plain-colored Tanager. Four grown birds, who could not be distinguished from each other, fed two nestlings, often coming in a little flock (Skutch, 1954:214-216).

Thraupis episcopus. Blue Tanager. In May of 1954, I discovered a nest with four eggs, which is twice the usual number found in El General, Costa Rica. It was attended by two females, who had a single mate—the only instance of bigamy that has come to my attention in this species. The dominant female, which was in better plumage than the submissive female, incubated when she wished; the other sat on the eggs when she was permitted to do so. This submissive bird spent much time hopping restlessly about the nest or preening close by it while her more forceful partner sat. She took over the eggs the moment the latter left and promptly made way for the dominant female when she returned. If the submissive tanager was slow in leaving the eggs, she received a mild peck from the dominant one. In four hours, the dominant female sat for 77.2 per cent of the time, which is about normal assiduity for a Blue Tanager. The submissive female incubated for 22.8 per cent of the time. The eggs were constantly covered, but the two females never incubated simultaneously. After the nestlings hatched, the male and two females fed them in perfect harmony, bringing 142 meals to the three nestlings in four hours. At least two young were fledged.

Ramphocelus passerinii. Scarlet-rumped Black Tanager. A full-grown, young bird, afflicted with paralysis, was fed at least once by two different females, one of whom appeared to be its own parent, while the other was the mother of fledglings just out of the nest (Skutch, 1954:127).

Piranga olivacea. Scarlet Tanager. A male fed young Chipping Sparrows until his own nestlings hatched (Hales, 1896).

Habia gutturalis. Red-throated Ant-Tanager. Immature birds sometimes help to build and more often to feed nestlings, probably later broods of their parents (Edwin Willis, *in litt.*, September 28, 1957).

Saltator maximus. Buff-throated Saltator. Although nests of this large, plain-colored finch are usually well separated, I once found two pairs nesting in neighboring coffee bushes, only eight feet apart. One female, who was clearly dominant, repeatedly chased her neighbor from the latter's eggs and nestling. The dominant female sometimes went to the other's nest to make sure that her rival was absent, and if she happened to be carrying food for her own nestling, she might give it to the offspring of the female she was trying to drive away. Twice I saw her feed her enemy's nestling, and once she brooded it for five minutes (Skutch, 1954:74).

Richmondia cardinalis. Cardinal. A juvenile, probably a female, whose age was estimated at about 78 days, brought food to a late nest of her own species. She also begged from the nestlings' parents and was occasionally fed by the male. The female parent tried to drive her away, yet on one occasion, while both rested on the nest's rim, she took food from the young helper and passed it to a nestling (Brackbill, 1944). A male Cardinal, whose nest had been destroyed, fed four fledgling American Robins a few days younger than his own lost nestlings. For a week, he was almost as active in bringing food to the young robins as were their own parents; and perfect harmony prevailed among the three attendants. After the replacement brood of the Cardinals hatched, the male apparently brought food to both families simultaneously. His mate took no interest in the robins (Logan, 1951).

Sometimes two female Cardinals lay in the same nest and attempt to incubate simultaneously, sitting side by side, facing in opposite directions. In one instance, these doubly incubated eggs failed to hatch; in another, they hatched (Hawksley and McCormack, 1951).

A male Cardinal fed seven goldfish, bringing food to them repeatedly for some days and standing on the pool's edge while he placed it in their open mouths, slightly raised above the water. This strangest of all the instances of "helpfulness" that have come to my attention is corroborated by an excellent photograph (Lemmons, 1956). See also Song Sparrow.

Pheucticus ludovicianus. Rose-breasted Grosbeak. A semicaptive male, arriving with food for his own nestlings, gave it to nestling grosbeaks in a neighboring nest, who were calling loudly because their parents had neglected them. He did this several times (Ivor, 1944a:99).

Pheucticus melanocephalus. Black-headed Grosbeak. An adult male with a deformed bill, which evidently made it difficult for him to feed himself, was fed by a female, by whose care he had apparently been kept in good condition for an extended period (Fox, 1952:160-161).

Passerina cyanea. Indigo Bunting. Juveniles fed still younger birds in captivity (Sanborn *in* Nice, 1943:79).

Carduelis mexicanus. House Finch. A nest in Colorado contained four half-grown American Robins, two newly hatched finches, and four finch eggs. It was attended by two adult robins and two female finches apparently mated to the same male, all five of which fed the young regularly. The large robins smothered their small nest mates. After the robins were fledged, the three finches continued to feed them. At another nest in the same locality, adult robins and adult finches fed young robins. There was no evidence, however, that the finches had laid eggs in this nest (Bailey and Niedrach *in* Bent, 1949:56).

Carduelis cannabina. Linnet. An injured adult was fed by a companion in a cage (Lack, 1953:82).

Fringilla coelebs. Chaffinch. Persistent calling for food by newly fledged Hawfinches (*Coccothraustes coccothraustes*) attracted a male Chaffinch, which fed them six times (Mountfort, 1957:91).

Pipilo erythrophthalmus. Rufous-sided Towhee. A female fed two young Mockingbirds (*Mimus polyglottos*), continuing this for hours. When she gave seeds, they were rejected, but insects were accepted (Westwood, 1946). A towhee and a Field Sparrow had nests 18 inches apart in the same tree, and both held nestlings of about the same age. The male towhee frequently fed the young sparrows and removed their droppings, and a parent sparrow likewise brought food to the nestling towhees (Hoyt, 1948). A towhee cared for a young Brown-headed Cowbird (*Molothrus ater*) which had been hatched in a nest of an Orchard Oriole, *Icterus spurius* (Neff, 1945).

Pipilo fuscus. Brown Towhee. A male whose own first brood had just become independent joined a pair of Cardinals in feeding three fledglings of the latter. These three adults worked together in complete harmony for about three weeks. A month after helping to feed the Cardinals, the towhee and his mate reared a second brood (Antevs, 1947).

Junco oreganus. Oregon Junco. When a pair of juncos and a pair of Bewick Wrens (*Thryomanes bewickii*) nested on opposite sides of the interior of the same garage, the juncos often chased the wrens as they came with food for their young. Yet, while his mate incubated, the male junco fed the nestling wrens and also cleaned their nest. The wrens did not try to drive away the juncos (Williams, 1942:245-246).

Spizella passerina. Chipping Sparrow. Juveniles about 39 days old fed a younger Redwinged Blackbird in captivity (Laskey *in* Nice, 1943:79).

Spizella pusilla. Field Sparrow. A case of reciprocal helpfulness with a Rufous-sided Towhee is given under the latter species.

Melospiza melodia. Song Sparrow. A pair of Cardinals and a pair of sparrows nested simultaneously in a nest built by the former and lined by the latter. Both females laid eggs and both incubated and brooded, the Cardinal sometimes sitting upon the sparrow. Three Cardinals were hatched and reared to nest-leaving, fed by all four of the adults cooperating closely. No antagonism between the Cardinals and Song Sparrows was noticed (Brackbill, 1952). A pair of sparrows helped a neighboring pair of American Robins to feed their nestlings and clean the nest, continuing until their own eggs hatched. One or two sparrows helped Yellow Warblers (*Dendroica petechia*) to feed a brood. When the female warbler was on the nest, she took the food from the sparrow and passed it to the nestlings. Two sparrows laid in the same nest and incubated alternately, then all four parents fed the eight young (various authors cited by Brackbill, 1952:306).

SUMMARY

A "helper" is a bird that assists in the nesting of an individual other than its mate, or feeds or otherwise attends a bird of whatever age that is neither its mate nor its dependent offspring. Helpers may be of almost any age; they may be breeding or non-breeding individuals; they may aid other birds of the most diverse relationships to them-

selves, including those of distinct species; and they may assist in various ways. The many recorded instances of this behavior are classified according to whether the helpers are immatures, innubiles (individuals sexually immature or inactive in a breeding season following that in which they hatched), nonbreeding adults, or breeding adults; whether they assist other birds of their own species or of different species; and whether their helpfulness is or is not associated with reproduction.

Aside from giving warning of the approach of danger, the most common mode of helpfulness is in feeding. Less often the helpers participate in nest building, incubation, and brooding. Some "mutual helpers" share rather equally in all the labors of building a nest and rearing a brood.

Contrary to earlier reports, when the young of several families gather in "crèches," the parents as a rule do not feed them indiscriminately, but each nourishes his or her own offspring.

Although interspecific helpers are most likely to attract attention, especially of the casual bird watcher, intraspecific helpers are more numerous in both species and individuals and they occur more regularly.

Examples of the several classes of helpers are given and the conditions which favor their occurrence are discussed.

Helpers point to the existence of much unused reproductive potential in birds and furnish additional evidence that their reproductive rate has, in many cases, been delicately adjusted to the circumstances of their lives rather than pushed to the limit of their capacity to rear sturdy offspring.

Helpers would doubtless occur far more frequently if superfluous assistants, and the increased activity inseparable from their presence, did not increase the likelihood of attracting predators to nests.

Brief accounts of the activities of helpers in over 130 species are given in an annotated list.

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THE HATCHING MUSCLE IN NORTH AMERICAN GREBES

By HARVEY I. FISHER

The "hatching muscle," *M. complexus*, extends from the dorsal lateral part of the anterior cervical vertebrae to the posterior dorsal surface of the skull. Its function is to raise the head. During the later embryological development in the chick the muscle increases rapidly in bulk, reaching its maximum size the day before hatching and diminishing in weight very rapidly thereafter. The pattern of elaboration of the egg tooth is chronologically similar. This concurrence of events has led to the theory that the muscle furnishes the power to bring the egg tooth sharply against the inner surface of the shell, and thus pip the shell, as the chick breaks its way out of the egg.

The developmental history, and even the presence or absence, of this muscle is unknown except in the chicken (Keibel, *Anat. Anz.*, 41, 1912:381-382; Pohlman, *Anat. Rec.*, 17, 1919:89-104; Fisher, *Auk*, 75, 1958:391-399). Therefore, it seems worthwhile to record any information on its occurrence in other species, even though the data are not definitive.

The purpose here is to report the gross morphological features of the muscle in the Pied-billed Grebe (*Podilymbus podiceps podiceps*), Horned Grebe (*Podiceps auritus cornutus*), Eared Grebe (*Podiceps caspicus californicus*), Western Grebe (*Aechmophorus occidentalis*), and in a few specimens of the Red-necked Grebe (*Podiceps grisegena holböllii*).

MATERIALS AND METHODS

Four kinds of grebes nest in the vicinity of the Delta Waterfowl Research Station at Delta, Manitoba, Canada. The Horned Grebe nests in numbers not far away in the "Pothole Country" near Minnedosa, Manitoba. Since there is great similarity between the eggs of the Pied-billed, Horned and Eared grebes, and between those of the Western and Red-necked grebes, no clutches of eggs were taken in the above-mentioned localities unless the incubating bird was identified as it left the nest.

Eggs collected for this investigation included: Western Grebe, 28; Red-necked Grebe, 4; Eared Grebe, 36; Pied-billed Grebe, 24; and Horned Grebe, 14. The eggs were numbered by clutches and incubated in the duck hatchery at Delta at 99.5°F. and approximately 60 to 70 per cent relative humidity. Samples from each clutch were taken when the eggs were first collected, to determine the stage of incubation since the eggs could not be candled.

It was not possible to determine the number of days an egg had been incubated, even upon examination. Further, the eggs in a grebe clutch may be several days apart in their relative development. Therefore, in all instances body weight has been used as the basis for defining the stage of development.

When the embryos were taken from the eggs, all the extra-embryonic membranes were removed, and in embryos "nearly ready to pip" and "pipping" the yolk was drawn from the body. Removal of yolk already intruded was done to insure uniformity and consistency; in earlier embryos the yolk was impossible to weigh accurately, and in any event it is not truly a part of the body. However, in comparing weights of embryos near hatching and after hatching one must recognize that the apparent increase in weight may not be real. Sample weights of intruded yolk, not included in the body weights before hatching, ranged from one to two grams in the small-bodied species and up to four grams in Western Grebes. Before it was weighed to the nearest tenth of a gram, the embryo was blotted on newspaper to remove surface moisture.

Hatching muscles were excised with iridectomy scissors and weighed in milligrams

on a Roller-Smith Precision Balance. Muscles from embryos weighing as little as three grams could be cleanly removed. All muscles were weighed within 30 seconds of removal, to prevent undue desiccation. It is also important to mention that removal took no more than a minute or two after the skin was slit above the muscle.

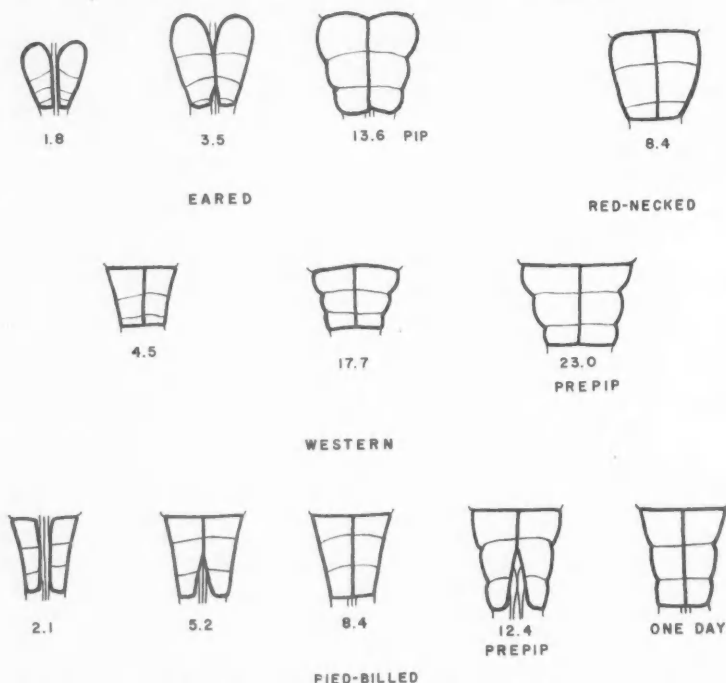


Fig. 1. Diagrams of dorsal views of the hatching muscles of grebes, twice natural size. Numerals below each drawing represent the body weight in grams.

After the muscles were taken out the embryos were preserved in formalin for later study of the egg tooth and other features.

RESULTS

Description of the muscle.—In all species examined the hatching muscle is a paired structure lying on the dorsal and lateral aspects of the anterior cervical region. Usually the left and right members of the pair of muscles have some degree of medial contact as will be discussed later. Each member arises primarily from the lateral ends of the transverse processes of the third and fourth cervical vertebrae, with some fibrous connection medially to the tips of the neural spines of these vertebrae. Its posterior tip may have fascial attachment to the deeper musculature. Insertion is superficial on the posterior crest of the skull; it extends laterally into the origin of *M. depressor mandibularis* on either side, and its anterolateral corner is overlapped by the posterodorsal tip of the hyoid apparatus.

Basically, *M. complexus* consists of three segments easily visible from early in incu-

bation until after hatching (fig. 1) except that just before pipping the segments may be obscured. In the Pied-billed Grebe one-third of the specimens possessed four segments, and two Eared Grebes showed this condition. The figures show that in grebes the segments are wider than long; they extend ventrally halfway around the neck. It is also evident that there is a gradient, anterior to posterior, of decreasing size of the segments. When a fourth segment is present, it is always smaller than the third segment. The anterior margin of the first pair of segments demonstrates some interspecific variation; in the Pied-bill the edge is straight, as is usually the case in the Western and Red-necked grebes. In the Eared and Horned grebes this border is convex anteriorly and frequently is notched in the middle of its length where the muscles of the two sides are in juxtaposition.

Development of the muscle.—Figure 1 delineates the qualitative features, and figures 2 and 3 the quantitative development, but some significant aspects should be mentioned. The Pied-billed Grebe will be used as the example and other species compared to it.

Specimens as small as 2.1 grams exhibited the muscle upon gross dissection. Segmentation visible to the naked eye first appears, faintly at this time, in the three small grebes, and at four grams of body weight in the Western Grebe. The segments become more and more distinct, until just before pipping when the dividing septa are obscured by the swollen condition of the muscle.

At the two-gram stage there is usually no medial contact between the muscles of the two sides (fig. 1); at three grams the medial contact begins anteriorly and proceeds posteriorly. Some three-gram specimens show complete medial contact, but this stage is not reached in most specimens until they weigh six or seven grams. Just before pipping, in the Pied-billed Grebe, a pair of narrow, band-like muscles, *Mm. biventer cervicis*, appears deep and medial to the two components of the hatching muscle (fig. 1). This development reduces the medial contact to the first and sometimes second pair of segments. Some Eared Grebes also have this secondary separation, but it was found in none of the embryos of Horned, Red-necked, or Western grebes. Continuous medial contact throughout the length of the muscle is evident in Horned Grebes after the six-gram stage and in Western Grebes after the 12-gram stage. By the time of hatching and for at least one day thereafter the muscles of the two sides are again in continuous contact in all species.

No major lymph glands were observed near *M. complexus*; in only two specimens (one Western Grebe just before pipping and a Horned Grebe that had just pipped) were there even a few lymph granules in the position of the lymph glands described for the chick by Fisher (*op. cit.*).

Despite the absence of nearby lymph glands, it is evident that there is lymph infiltration of the muscle in grebes. Beginning at seven grams in the Pied-billed Grebe, at eight to ten grams in the Western, and at five or six grams in the Eared and Horned grebes, the muscle assumes a faint straw color. Infiltration and the resulting turgidity reach their peak just before pipping. At this time the lymph color is present even in the lateral and ventral cervical muscles and in *M. depressor mandibularis*. In those specimens where there was secondary separation of the two sides of *M. complexus*, lymph was evident medially. No lymph was observed subdermally, superficial to the muscle. The muscle complex appears as a nearly solid, swollen block of tissue with the segments only faintly discernible. During pipping and hatching the lymph begins to disappear. In day-old Pied-billed Grebes the lymph color was receding, and in a Western Grebe two days old the muscle was pinkish red as were other cranial and cervical muscles.

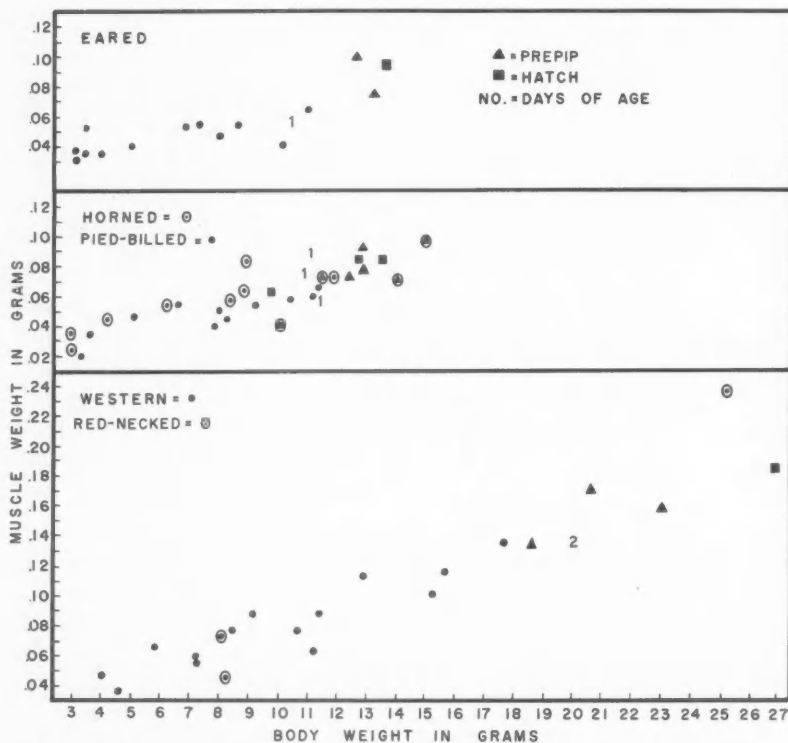


Fig. 2. Scattergram illustrating gradual increase in weight of the hatching muscle in grebes.

Comparison of the blood vessels serving the hatching muscle and those serving the rest of the neck revealed that the former were much larger and more obvious, particularly during the prepping and pipping stages.

Figure 2 shows that in all the species there is a gradual, and straight-line, increase in the weight of the hatching muscle as the body weight increases. There is no major upsurge in the weight of the muscle prior to hatching and no observable decline during hatching or the first day, although the data are few in the latter instance.

In figure 3, where muscle weight is expressed as per cent of body weight, it may be observed that the relative weight of the muscle is greatest early in development (at 3 to 5 grams) in all grebes studied. Thereafter it declines in relative weight until shortly before the embryo starts to pip. The scattergram for the Pied-billed, Eared, and Western grebes illustrates the increase in the weight of the muscle before pipping. Note that the Red-necked and Western grebes have, in general, a relatively larger muscle throughout development than do the smaller Pied-billed, Horned, and Eared grebes. Particularly is this true at the "ready to pip" stage. There is close similarity in relative muscle weight among the small grebes at this stage. In the three species (Western, Eared, and Pied-billed) for which "just-hatched" specimens were available the relative muscle weights are essentially the same.

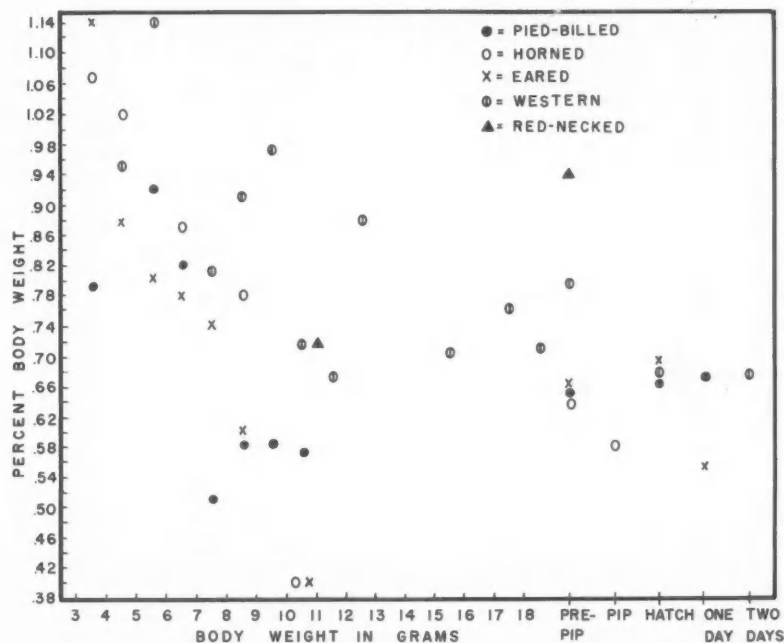


Fig. 3. Scattergram showing average size of hatching muscle relative to body weight of grebes. Number of specimens may be obtained from figure 2.

The few data indicate that Pied-billed Grebes hatch at 10 to 14 grams in body weight, Horned Grebes between 13 and 14 grams, and Western Grebes at about 28 grams.

The egg tooth.—In Eared Grebes at 0.63 grams of body weight, the egg tooth is not formed, but there may be a slight elevation at the future site of the tooth on the culmen. At 0.80 grams the tooth is present and is a contrasting white in color (fig. 4). By the time the embryo is one gram in weight an obvious tooth, 0.5 mm. in diameter, is present. Gradual increase in height and diameter continues until hatching. Note in the figures that the egg tooth is not so much a projection upward or dorsal as it is a forward extension parallel to the long axis of the bill. During the first and second days after hatching the tooth begins to disappear (fig. 4).

The only exception to the above in grebes is that in the Western Grebe the egg tooth was not found until the one-gram stage of body weight.

DISCUSSION AND SUMMARY

The hatching muscle in grebes is grossly similar in its morphology to the muscle in the chicken (Fisher, *op. cit.*). However, in grebes the segments are much wider than long, and they extend farther laterally. This lateral extension is least evident in the Pied-billed Grebe.

Virtual absence of the lymph glands on the dorsolateral surface of the neck, coupled with massive lymph infiltration of cervical muscles, leads to the conclusion that lymph

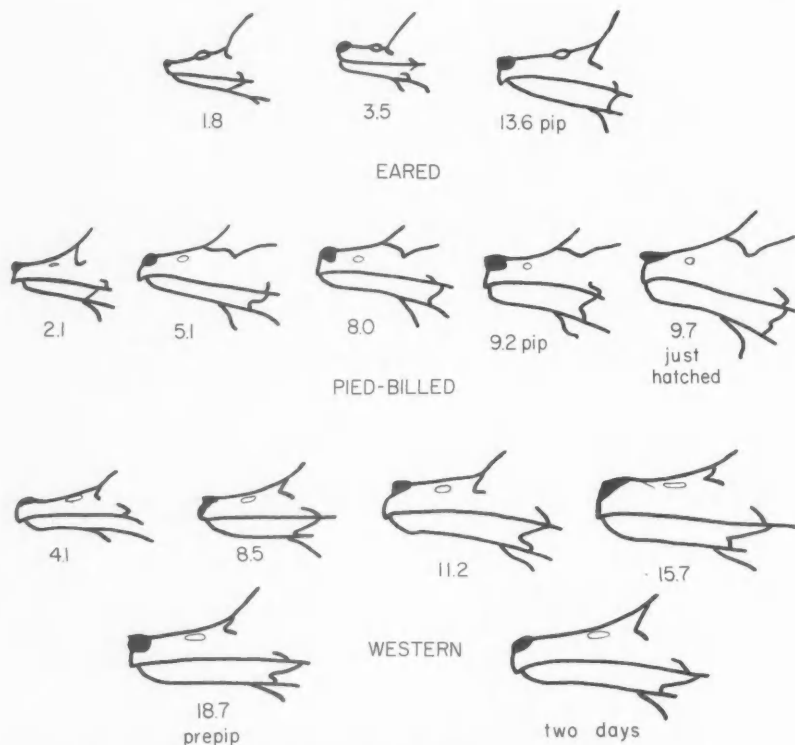


Fig. 4. Sketches of the development of the egg tooth in grebes, twice natural size.

moves in from some more distant glands. Much of the increase in weight of the hatching muscle results from increases in lymph content.

Although Pohlman (*op. cit.*) believed that the lymph hindered the activity of the muscle, it is my thought that the lymph may be the carrier for large sources of energy—glycogen and even fat. The relatively larger blood vessels serving the hatching muscle in the grebes also indicate that lymph infiltration is not a "biological accident," as one could perhaps theorize when the glands overlie the muscle as in the chick. There is no question that the lymph disappears rapidly during the pipping and hatching process. This depletion might result from use of the materials for energy during this critical time or it might simply be regression from the muscle due to increased pressures during active contraction. Some evidence for the first hypothesis lies in the frequent observation that in chicks and in ducks (Fisher, MS) eggs which are pipped and do not hatch within 24 hours usually do not hatch successfully. It seems plausible to believe that the energy resources were depleted before hatching could be accomplished. Fisher (Auk, 75, 1958: 394) found that the hatching muscle in chicks that pipped but could not emerge was significantly smaller than in "normally pipped chicks."

Although the absolute weight of the muscle increases gradually throughout the

period of development, it is relatively greatest early in incubation. This phenomenon is a result of the initial, more rapid, development of the cephalic portion of the embryo. My study of the chick (Fisher, *op. cit.*) did not include material prior to 15 days of incubation and thus this early development was not observed. It is not until shortly before pipping that the muscle shows its phenomenal increase relative to body weight.

The relative weight of the muscle is greater in the larger Western and Red-necked grebes, and there is close agreement in relative size between the Pied-billed, Horned, and Eared grebes. Note, however, that after hatching the relative size of the muscle in the Western Grebe is the same as in the Eared and Pied-billed grebes. This leads to the supposition that size of the egg and composition of the shell may be factors in determining muscle size. All grebe eggs observed during this study were soft to the touch, chalky, and rather easily broken, but eggs of the Western and Red-necked grebes had harder shells. Further, although grebe eggs are normally moist as a result of proximity to the water and the habit the incubating bird has of covering the eggs with wet vegetation, eggs of the two larger species never seemed as wet and frequently there was only a "token" covering of vegetation. Non-attended eggs of the smaller grebes were rather uniformly covered. It is realized that extent of covering of the eggs depends in part on the manner in which the incubating bird is flushed from the nest, but there seems to be an interspecific difference in the grebes.

Comparison of relative muscle weights in the chick and in the grebes, at the pre-pipping and hatching stages, further enforces the view that muscle size is related to egg size and to composition of the shell. Relative muscle sizes in the grebes are only one-third to one-half as great as in the chick (Fisher, *op. cit.*:394). Studies of the structure and composition of the shell are sorely needed; virtually all of the data in the literature pertain to the chick.

The massive development of the muscle is transitory, the muscle is not; this point was not clear in my paper of 1958.

These further studies of *M. complexus* lead me to believe that the muscle represents all or part of the caput portion of *M. cucullaris*.

The egg tooth first appears, upon gross examination, when embryos of Eared, Pied-billed, and Horned grebes are between 0.70 and 0.80 grams in body weight. It is present in Western Grebes only after the one-gram stage. Once hatching has occurred the tooth begins to regress rapidly.

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Southern Illinois University, Carbondale, Illinois, October 2, 1960.

COMMENTS ON TYPES AND TAXONOMY IN THE JAY GENUS APHELOCOMA

By FRANK A. PITELKA

During a year's stay in Europe in 1957-58, I was able to study types and other specimens of the genus *Aphelocoma* in collections of British and continental museums. These opportunities permitted me to try to clear up some points left unresolved in my revision of that genus (Pitelka, 1951).

Of the types examined, two provide information which requires changes in racial taxonomy. These are *Cyanocitta superciliosa* Strickland 1845, which applies to the Scrub Jay (*Aphelocoma coerulescens*), and *Garrulus sordidus* Swainson 1827, which applies to the Mexican Jay (*Aphelocoma ultramarina*). For seven more types, information given here supplements that provided in the earlier paper. Details regarding any of these types, such as museum numbers or collecting locality, available in my 1951 paper, are omitted when they are not vital to the discussions in this paper. Page references given here without additional information regarding source pertain to my 1951 paper. Methods of taking measurements are described in that paper on page 202.

Finally, racial taxonomy of *Aphelocoma ultramarina* and the use of subgenera in the genus *Aphelocoma* are discussed briefly.

TYPES REQUIRING TAXONOMIC CHANGES

CYANOCITTA SUPERCILIOSA Strickland 1845 [= ? Indeterminate]

The type of *superciliosa* Strickland at Cambridge University was examined by van Rossem (1933) and considered to represent the race of the central valley and foothills of interior California known earlier as *immanis* Grinnell (see p. 396). Van Rossem brought the type to the British Museum and compared it there with the "ample series of all the races." He added, "It agrees minutely with specimens from the Sacramento Valley." No critical details are given regarding color or size, and it is merely stated that Strickland's specimen "certainly is neither *californica* nor *oocleptica*." These comparisons were repeated by me in January, 1958, and reconsidered several times after that at the British Museum. I disagree with van Rossem. In brief, the specimen, a first-year individual, is too purplish and too dark to represent the interior race. It belongs to one of the coastal races (*californica*, *oocleptica*, or *caurina* of my revision), but no definite determination can be made.

In the following discussion, "*superciliosa*" in quotation marks will refer to the populations bearing this name as delimited in my revision (pp. 248, 395), in Grinnell and Miller (1944:287), and in the A.O.U. Check-list (1957:373).

The sex of the type is unknown. Among first-year individuals, as among adults, extremes in head coloration and in development of the collar pattern, considered together, can be identified as to sex, but in these characters Strickland's specimen falls into the overlap between sexes. But, as noted by van Rossem (1933), the specimen is in fresh, unabraded plumage and in good condition, so that informative comparisons can still be made.

The pertinent material in the British Museum available to van Rossem consisted of the following:

	Adults	First-year individuals	Juveniles
<i>A. c. oocleptica</i>	6	2	
<i>A. c. californica</i>	7	3	1
<i>A. c. "superciliosa"</i>	4	2	1
<i>A. c. obscura</i>	9	5	1

Among the specimens of "*superciliosa*," only five were suitable for comparison with the type: three from the central Californian valley (an adult male, an adult female, and an unsexed first-year individual, all from Stockton), and two from the central Sierra Nevada foothills (an adult female from Amador County and an unsexed adult from Nevada County). The type, a first-year specimen, was more purplish to my eyes than all of these five specimens. Mr. Derek Goodwin, ornithologist at the British Museum, kindly performed the same comparisons at the same time and place as mine and agreed about the direction of difference in the first four specimens, but the fifth (an adult) he considered to be similar to the type.

As is brought out in my revision (pp. 209-214, 279), in *Aphelocoma coerulescens* there is a four-step progression from adult males, through first-year males and adult females, to first-year females in average hue and intensity of purplish-blue coloration. These age and sex differences are most strongly expressed on the head and chest. Thus, when a first-year specimen, without regard to sex, matches the average purplishness of a series of adults comprising a geographically circumscribed sample, or when such a first-year specimen is more purplish than adults from that sample, the probability of its having come from the area represented by the sample is low. This is the conclusion drawn from the previously mentioned comparison of Strickland's specimen with the available and usable material of "*superciliosa*" in the British Museum.

Comparison of Strickland's type with specimens of the coastal races *californica* and *oocleptica* add support to this conclusion. Compared with nine specimens of *californica* from Monterey and Santa Barbara counties, the type was more purplish than three adult females and one first-year female; similar to one first-year male and one first-year female; and less purplish than three adult males. Compared with eight specimens of *oocleptica* from Marin, Contra Costa and San Francisco counties, the type was more purplish than one first-year female; similar to one adult female; and less purplish than four adult males, one first-year male, and one adult female.

In other words, on the basis of comparisons made at the British Museum, the type falls easily within the limits of color variation of *californica* and *oocleptica*. In particular, omitting adult males now, this unsexed first-year specimen is similar to or more purplish than all coastal specimens of both races (of a combined total of 10) except the two *oocleptica* just mentioned. These facts further increase the probability that the type was obtained along or near the coast. It follows that because of the similarity in color of *oocleptica* and southern populations of *caurina* (p. 225), including that near Fort Ross, Sonoma County, the type would also fall within the color variation of the latter.

Measurements of the type are as follows: wing, 116 mm.; tail, 124; bill length, 19.7; bill depth, 9.3; tarsus, 40.7. These fall within the limits of first-year age classes of all three of the coastal races. They also fall within the combined limits of first-year age classes of the population in the Sacramento Valley ("*superciliosa*," part). In other words, evidence from a consideration of mensural characters is neutral. Other interior populations, belonging to any race of the "*californica*" group of races (p. 207), are not relevant to the problem here because in color, size, or both, their variational patterns exclude Strickland's specimen, and because circumstances of historical explorations which produced that specimen also exclude those populations.

Strickland obtained his specimen from J. F. Brandt, St. Petersburg, in 1844, and it is now necessary to consider its possible source.

Historical background for Strickland's specimen.—An entrée into the literature on scientific exploration along the central Californian coast before 1844 is provided by Alden and Ifft (1943) and by Ewan (1955). Russian settlement and travel in California

are summarized compactly by Essig (1933), and a number of scientists are mentioned by him. A useful resumé of the historical setting of early explorations along the Pacific coast is given by Hammond (1955). Various other sources, both published and in manuscript, in the Bancroft Library of the University of California, were utilized in developing the historical background for this discussion; but I shall cite only those immediately relevant to the problem of assigning Strickland's name.

Either of two views may be taken in disposing of *Cyanocitta superciliosa* Strickland 1845: (1) It is based on a specimen obtained by the Russians themselves and sent to St. Petersburg, from where Brandt sent it to Strickland. Or (2), it is based on a specimen among others obtained by several collectors of other nationalities who visited the central Californian coast prior to 1844; such specimens were sent to European centers, from one of which Brandt obtained the jay sent to Strickland in 1844.

Taking the first of these possibilities, so far as I can make out, two voyages clearly yielded specimens of birds brought safely to St. Petersburg: The first was a voyage of Otto von Kotzebue (1830). This, his second world voyage, included the naturalist Eschscholtz, who, in a "Review of the Zoological Collection" appended to Kotzebue's account, reports an unitemized total of 165 specimens of birds obtained on the expedition. Although he mentions several Californian birds, the jay is not one of them.

The second was the long visit of Vosnesensky, who remained in central California from July, 1840, to September, 1841 (see Essig, 1931:777-779 and references cited in footnotes; see also Blomquist, 1951). Vosnesensky was evidently the last of Russian explorers collecting in central California, as the colony was closed down at the end of 1841.

As can be determined from a reconstructed itinerary for Eschscholtz, most of his time was spent in the immediate vicinity of San Francisco Bay. For Vosnesensky, only bits of information are available in publications, mainly in conjunction with collection localities of insects, which received a lot more formal taxonomic attention once they arrived in St. Petersburg than did the birds he obtained. This is reflected by the fact that there is no mention of Brandt or Vosnesensky in Grinnell's (1909, 1924, 1939) bibliographies of Californian ornithology. Still, what evidence we have tells us that Vosnesensky also spent most of his time along the coast, about Fort Ross, Bodega Bay and San Francisco Bay. Like Eschscholtz, he visited the Sacramento Valley and apparently only once.

A recent letter from Professor A. I. Ivanov of Leningrad provides some critical facts. Following his departure from Fort Ross, Vosnesensky spent the period November, 1841, to March, 1842, in a voyage to Baja California, visiting Loreto, Carmen Island, and Puerto Escondido on the gulf side of the peninsula. There are five specimens of *Aphelocoma coerulescens* taken by Vosnesensky still in the Leningrad collections: two are without original labels; the other three were taken, respectively, in "California" [presumably referring to the Spanish part of the coast around 1840, and not to New Albion north of San Francisco Bay]; at "Nova Helvetia" [later Fort Sutter, now Sacramento]; and at Escondido, mentioned above. We therefore have definite evidence that Vosnesensky collected a jay in the Sacramento Valley, but this does not alter the arguments regarding Strickland's specimen. The latter plus two more specimens in Leningrad are without original labels and may have been taken by Vosnesensky at some base of operations such as Fort Ross where he did not bother with labels, but there is no way of determining this one way or another. It may be added that the specimen from Nova Helvetia was taken March 16, 1841, whereas Strickland's specimen, "in good condition and in fresh, unabraded plumage" (van Rossem, 1933), was clearly taken in one of the fall months not long after the annual molt.

We therefore have these facts: (1) Strickland's specimen is clearly assignable to a coastal race; and (2) from evidence on Eschscholtz's and Vosnesensky's travels, it is clear that they both spent most of their time coastally, within the ranges of *A. c. oocleptica* and *A. c. caurina*; and (3) for Vosnesensky there is definite evidence that he collected Scrub Jays in areas falling within the distributions of at least three, and possibly four or five presently recognized races.

Van Rossem's (1933) designation of the type locality as the Sacramento Valley and his assignment of the type to the race of the interior earlier known as *immanis* (Swarth, 1918) must both be rejected. Assuming, as van Rossem did, that Brandt obtained the specimen from one of the Russian expeditions, there is no basis now on which one may definitely restrict the type locality and assign the type to one of the recognizable races. *Cyanocitta superciliosa* Strickland 1845 may be an older name for *Aphelocoma californica oocleptica* Swarth 1918; if new evidence becomes available to justify use of Strickland's name, no particular problem arises if this change is made because of the revision of the concept of the interior Californian race of the Scrub Jay developed beyond under "Taxonomic changes." If, however, *Cyanocitta superciliosa* Strickland 1845 proves to be an older name for *Aphelocoma coerulescens caurina* Pitelka 1951, then another one of those regrettable name transfers faces us, and frankly I do not see what would be accomplished by it. Finally, a slim possibility remains that *Cyanocitta superciliosa* Strickland 1845 refers to *Garrulus californicus* Vigors 1839.

This brings us to the second of two views that may be entertained in the disposal of Strickland's name. It must be acknowledged that in the first decades of the 19th century, collectors other than Russian ones were visiting central California, and the specimen obtained by Strickland from Brandt, now without date or place of collection, could have come to the latter from Berlin, London, Paris, or some other center. Between 1826 and 1837 central Californian birds were brought to Europe by Collie (on Beechey's voyage), Botta, Deppe, and Neboux (see Alden and Ifft, 1943; Ewan, 1955). Finally, from reports in the 1840's by Brandt in the Bulletin Scientifique de l'Academie Imperiale des Sciences de St. Petersburg (as also the article about Vosnesensky by Gilson translated from the Russian in full in Essig, 1931:778-789), it is evident that there was an exchange traffic between St. Petersburg and at least Berlin and London. Indeed, in the Compte Rendu for 1843 appended to the Bulletin, Strickland himself is mentioned in connection with some specimens of Siberian birds sent to England. As mentioned earlier, Strickland's specimen of the Scrub Jay from Brandt has no locality data, and unless some very specific information turns up in the archives of the Leningrad Museum, there is no hope of resolving the present dilemma. All circumstantial evidence points to the likelihood that Strickland's specimen was one of those taken by Vosnesensky. Ivanov (*in litt.*) subscribes to this view, and indirectly Stresemann (*in litt.*) does likewise by expressing doubts that any specimens taken by Botta, Neboux, and especially Deppe were ever acquired by the St. Petersburg museum.

Thus, at present, we have no more than strong circumstantial evidence with which to associate Strickland's specimen with Vosnesensky, and no good evidence as to where it really came from. In this situation I consider it best to follow Hellmayr (1934:52, footnote). He states, "There being no means of telling whence the specimen described by Audubon [under his *Corvus ultramarinus*] originated, *C. superciliosa* [offered by Strickland as a new name for *Corvus ultramarinus* Audubon 1838] should not come into use and may stand as a doubtful synonym of *G[arrulus]. californicus*, with which it was subsequently identified by Strickland [1845] himself."

Taxonomic changes.—The evidence that *Cyanocitta superciliosa* Strickland 1845

is inapplicable to the race of interior central California and adjacent areas requires an adjustment in the names used for the coastal or "*californica*" group of races. In developing the rationale for this adjustment, I must emphasize at the outset, as others have in recent years, that application of trinomials to a complex of nonconcordant clines is necessarily an arbitrary procedure serving the practical needs of museum taxonomy, and little more. A margin of mistreatment to *all* the facts collectively is unavoidable.

In the following discussion, the main features of character geography are reviewed for the Pacific coast races of the Scrub Jay. I hope that the streamlining needed to make this review brief will place into good perspective the main facts with which I justify my revised application of trinomials to those races. For background details and original documentation, see Pitelka, 1951:209-269, 389-398.

In the discussion of clines, the extremes of color and size among the Pacific coast races will be denoted by appropriate and easily understood adjectives. But use of the word "intermediate" requires comment. It refers not to intergrades but to taxonomically recognizable mid-intervals of a total range of geographic variation for particular characters of color or size within the entire complex of Pacific coast races. Thus the coastal race of Scrub Jay in central California, *A. c. californica*, is in this sense more or less intermediate in both color and size between the large, pale race of the San Joaquin Valley and the small dark race of northern Baja California.

Omitting peripheral races not relevant to the problem before us, there is a south-to-north color trend along the coast from very dark in northern Baja California (*A. c. obscura*) to intermediate in central California (*californica*). This reverses north of Monterey Bay, and there is then a gradual darkening which reaches an extreme in southwestern Oregon (*caurina*). Eastward and inland there are lighter and paler populations (*immanis* versus *caurina* in the north; "*superciliosa*" versus *californica* in central California). Thus, from central California northward, we have a cline along the coast giving basis for two racial names, and a cline interiorward giving basis for a third. Along a south-to-north axis, the interior populations more or less parallel or reflect the coastal cline so that color of the northern interior populations (Willamette Valley, Oregon) is similar to that of the central coastal ones (Santa Barbara to Monterey counties, California).

In size variation, the situation is somewhat simpler. North of the range of *obscura*, the coastal populations are intermediate in size, the interior ones are significantly larger. One complication arises, however; populations similar in size to those of the interior interrupt the consistency of size characteristics along the coast in the San Francisco Bay area. Thus, using size differences, there is basis for two racial names, one applying to coastal populations, the other to interior populations but including the Bay-region intrusion.

It is possible to accommodate the change provoked by the new evidence regarding *Cyanocitta superciliosa* Strickland 1845 in a reasonably simple way, with appropriate emphasis on the facts of character geography and without introducing a new name. I propose that populations of interior California previously called "*superciliosa*" be combined with those of the San Francisco Bay area to be named collectively *Aphelocoma coerulescens oocleptica* Swarth 1918. In my revision, *oocleptica* was recognized as a segment in the coastal color cline (*californica* to *caurina*) having, however, the size characteristics of interior populations. The A.O.U. Check-list (1957) recognizes one less race along the Pacific coast than I did; but in letting *oocleptica* stand as originally delimited geographically by Swarth, the check-list arbitrarily sets aside evidence I gave (1) that coastal populations north of Marin County do not show size characteristics that Swarth

attributed to them (see pp. 219, 389); (2) that at their northern end, coastal populations become dark (see pp. 223, 225) while Swarth used only size distinctions in justifying the description of *oocleptica*; and (3) that the size distinctions drawn by Swarth (1918, table opp. 408) between *oocleptica* and *californica* were exaggerated by his failure to segregate age classes, which results then led him to consider *obscura* a synonym of *californica* (see p. 393).

I will now go along with the A.O.U. Check-list in recognizing only four races where earlier five were recognized. My reasons are as follows: Coastally, we have populations intermediate in size, but some are intermediate in color (central coast) and others are dark in color (north coast). This justifies use of the names *californica* and *caurina*. Interiorward, we have populations large in size, but those to the south are pale in color while those to the north are intermediate in color. Atop the coast-to-interior size cline, there is, in the interior, a south-to-north increase. This justifies use of the name *immanis* to the north and, now, as the only available name, *oocleptica* to the south to include both interior populations and those of the San Francisco Bay region inserted between populations of smaller size to both north and south.

This arrangement may seem anomalous because of the fact that the type locality of *oocleptica* is in Marin County and that this name has always been associated with coastal populations. But for reasons just given, the overall geographic variation is more correctly reflected in an arrangement which links the San Francisco Bay region with interior populations to stress size similarities and the nonconcordance in clines along the coast. The name then applied to these interior populations also serves to denote the coast-to-interior color cline.

The only alternative to decisions presently offered above is to rename the interior populations while retaining *oocleptica* as defined in my monograph. This would only burden the trinomial nomenclature of the Scrub Jay in a futile way. Trinomials, if their use is to be continued, cannot succeed in denoting more than the main features of character geography in a given species; and in the Pacific coast races of the Scrub Jay, this can be accomplished with the available names.

The reduction of the number of races to the north within the coastal group of races requires that this be carried one step further if the application of trinomials within the species be reasonably consistent. As with *oocleptica* Swarth 1918, *cactophila* Huey 1942 proves not to be so well marked as claimed by the original describer chiefly because age-classes were not distinguished (p. 242). In view of the complex of minor geographic variations now subsumed by the name *oocleptica*, it is appropriate to revert to Hellmayr's (1934:53) conception of the race *hypoleuca* and to include *cactophila* thereunder.

Taxonomy of the remaining races of *Aphelocoma coerulescens* to the east and south, that is, to the Rocky Mountains and southern México, is not affected by the arguments of this paper.

The recognizable races comprising the coastal or "*californica*" group then stand as follows:

- Aphelocoma coerulescens immanis* Grinnell 1901
- Aphelocoma coerulescens caurina* Pitelka 1951
- Aphelocoma coerulescens oocleptica* Swarth 1918 (including "*superciliosa*"
of the A.O.U. Check-list, 1957, not of Strickland, 1845)
- Aphelocoma coerulescens californica* (Vigors) 1839
- Aphelocoma coerulescens cana* Pitelka 1951
- Aphelocoma coerulescens obscura* Anthony 1889

Aphelocoma coerulescens hypoleuca Ridgway 1887 (including
cactophila Huey 1942 of the A.O.U. Check-list, 1957)

Aphelocoma coerulescens insularis Henshaw 1886

GARRULUS SORDIDUS Swainson 1827 [= *Aphelocoma ultramarina ultramarina*
(Bonaparte), p. 416]

In my revision, I followed Hellmayr (1934:56) in the use of the name *sordidus* and not van Rossem (1939), who reported that the type represents the nominate race. In January, 1958, I borrowed Swainson's specimen from the collections of Cambridge University and compared it with specimens in the British Museum and with the colored plate published by Swainson some years after the original description (1832:pl. 86). The type is an unsexed adult and unnumbered. After reviewing this matter several times in the British Museum, I now subscribe to the arguments given by van Rossem (*loc. cit.*) and also by Brodkorb (1944:401) regarding the disposal of the name *sordidus* Swainson.

Originally (pp. 413-416), I argued that the plate published by Swainson, in combination with other circumstances to be mentioned beyond, justified adherence to Hellmayr's views. The colored plate, however, is not an accurate depiction of the specimen now considered to be the type: the upper parts are painted too blue (not purplish enough), the back in particular is too blue (not grayish brown enough, with merely a purplish blue overcast), the light wash over the venter is too blue (this color was probably intended to suggest light gray, the actual color, although now the specimen is dirty). My measurements are as follows: wing, 175 mm.; tail, 158; bill length, 19.6; bill depth, 10.0; tarsus, 43.9. In color as well as size characters, the specimen clearly represents *A. u. ultramarina*.

There still remain at least three unresolved points: (1) Whether Swainson had one or more than one specimen in the interval from 1827 to 1832; (2) whether the first of them is the one now at Cambridge, and (3) whether that first specimen, granted that it is the specimen now in Cambridge, could have come from Real del Monte. It is highly unlikely that the Cambridge specimen could have come from Real del Monte, as the evidence now available places that locality within the race neighboring to the north; and I accept Brodkorb's (1944:401) reasons for restricting the type locality of *sordidus* Swainson to Río Frio, state of México. Any more discussion regarding points (1) and (2) or other details is futile. We have a specimen of Swainson's regardable as the type of *sordidus* and identifiable as to race. The facts given here and the circumstantial considerations set forth by van Rossem (1939) and Brodkorb (1944) permit a nomenclatural action more definite than any other. Moreover, the population of the southern part of the Sierra Madre Oriental bore a well-documented name for 35 years prior to the change promoted by Hellmayr. Therefore, in agreement with van Rossem and Brodkorb, *Garrulus sordidus* Swainson 1827 is here regarded as a synonym of *Corvus ultramarinus* Bonaparte 1825, and *Aphelocoma ultramarina sordida* of my revision (pp. 338, 412) and the Mexican check-list (Moore, 1957:124), occurring in San Luis Potosí, Hidalgo, Querétaro, and Guanajuato, should retake its former name *potosina* Nelson.

SUPPLEMENTARY INFORMATION ON OTHER TYPES

Corvus ultramarinus Bonaparte 1825 [= *Aphelocoma ultramarina ultramarina* (Bonaparte), p. 416]

A specimen of *A. u. ultramarina* in the Rijksmuseum van Natuurlijke Historie at Leiden was considered by van Rossem (1942) possibly to be the type. I examined it in January, 1958, but have little to add to the discussions in his and my papers (see p. 417). My measurements are as follows: wing, 177 mm.; tail, 172; bill length, 19.6; bill depth, 9.7; tarsus, 42.3. The specimen is an adult, not a

first-year individual as reported earlier by van Rossem in notes quoted in my paper (p. 417). Its status as a type remains doubtful, and without new evidence the situation remains as reported in my 1951 paper.

Cyanocitta ultramarinus Bonaparte 1850 [= *Aphelocoma ultramarina potosina* Nelson, p. 412 ("sordida")]

Another specimen at the Leiden Museum discussed under *A. u. ultramarina* in my revision (p. 417) is the basis for the first name given above, but it is not a synonym of *ultramarinus* Bonaparte 1825. Van Rossem's notes (quoted p. 417) led him to assign it to *wollweberi*, but data on color were lacking. I consider that it clearly represents *A. u. potosina*. The pileum is strong blue (duller and lighter blue in *wollweberi*); the back is strongly suffused with blue (not so in *wollweberi*); the sides of the face are a clear blue similar to that on the crown and contrasting strongly with the white throat (not so in *wollweberi*); the chest is crossed by a broad band of dull light blue (frequent in *potosina*, rare in western Mexican races). With regard to evaluation of color characters, van Rossem was handicapped for lack of adequate comparative material at Leiden, and moreover did not have benefits of either recent, concentrated restudy of specimens of *Aphelocoma* such as I had in London and Paris or of such background experience as my revision provided. My measurements agree closely with those of van Rossem: wing, 164 mm.; tail, 140; bill length, 19.5; bill depth, 10.0; tarsus, 42.4. These collectively fall into the ranges for *potosina* (p. 339) and not of *wollweberi* of Zacatecas (p. 331). Finally, it is doubtful that specimens from the Sierra Madre Occidental (that is, of *wollweberi*, *sensu stricto*) were available to Bonaparte at the time he made his studies. The above name should therefore appear in the synonymy of *potosina* Nelson and not of *wollweberi* Kaup.

Pica sieberii Wagler 1827 [= *Aphelocoma ultramarina ultramarina* (Bonaparte), p. 416]

There is an unsexed adult specimen in the Munich Museum labelled as a cotype of *Pica sieberii* Wagler and listed by Hellmayr (1934:57). I examined it in April, 1958. The specimen clearly represents the dark, large race of southeastern México. Its measurements are wing, 180 mm.; tail, 170; bill length, 20.8; bill depth, 10.6; tarsus, 41.4.

Aphelocoma wollweberi Kaup 1854 [= *Aphelocoma ultramarina wollweberi* Kaup, p. 408]

Hellmayr (1934:56) states that the type is in the Darmstadt Museum, but in my paper, the type is designated "unknown." This discrepancy may have resulted merely from my oversight of Hellmayr's information, or it may have resulted from an impression based on notes taken by A. J. van Rossem in 1939 on a specimen in the Brussels Museum which he thought might be the type. I do not know now why the discrepancy occurred. The bird collection of the Darmstadt Museum was destroyed by bombs during World War II, and during my visit there in April, 1958, I found no information which could throw any light on the supposed type.

The specimen in the Brussels Museum reported by van Rossem to be one of Kaup's original specimens from Zacatecas and discussed in my revision (p. 409) was examined by me in Brussels. It is an unsexed adult (no. 5250) collected in late spring or early summer; it was entered in the catalog of the museum on November 9, 1855. My earlier comments left racial assignment of this specimen undecided for lack of information regarding color, and the choices left open were *A. u. "sordida"* or *A. u. wollweberi*. The blue coloration of the specimen is pale and grayish and within the range displayed by *wollweberi*. My measurements of it fall close to those of van Rossem: wing (chord), 154 mm.; tail, 130; bill from nostril, 17.8; bill depth at nostril, 8.4; tarsus, 37.4. The measurements, even without the datum of sex, also place the specimen into *wollweberi* (my table 49, p. 331) and not "*sordida*" (my table 54, p. 339). In other words, there is no reason now for doubting that the specimen represents the Zacatecas population of the race *wollweberi*.

In his original notes, van Rossem expressed the view that the Brussels specimen could even be Kaup's type because of the agreement between this specimen and Kaup's original description with regard to shortness of the central pair of rectrices. All evidence now available supports van Rossem's suspicion that the Brussels specimen is at least a cotype. This possibility cannot be considered further without some new evidence from journals, catalogs, or correspondence about the history of the specimen now in Brussels and the one said by Hellmayr to have been in Darmstadt. As Kaup gives inclusive measurements for *wollweberi* in his table (see p. 409), he evidently had at least two specimens.

One question is whether Kaup's type was in Darmstadt in the decade prior to 1940. As the museum is supposed to have contained additional types of North American birds such as those described by Bonaparte, Bechstein, Kaup, and Malherbe, there remains some hope that the uncertainty regarding the present whereabouts of the type of *wollweberi* Kaup may be cleared up.

Aphelocoma gracilis G. S. Miller 1896 [= *Aphelocoma ultramarina gracilis* G. S. Miller, p. 411]

The type, in the British Museum, is number 1906.12.7.3736; earlier it was number 230,470 in the Museum of Comparative Zoology. It is an unsexed adult, but in his original description, Miller (1896) states it to be a male. In his catalog (now deposited in the British Museum), it is also listed as a male. The type now lacks an original label. My measurements indicate the type to be exceptionally small for a male and suggest it may have been a female: wing, 146 mm.; tail, 126; bill length, 17.5; bill depth, 8.0; tarsus, 34.9 (compare with data in table 50, p. 333).

The name *gracilis* was used by me to apply to the smallest of three western Mexican races occurring from north to south in the Sierra Madre Occidental, but the original sample of that race was small. Additional specimens from northwestern Jalisco and Nayarit examined by me in recent years confirm the racial diagnosis given in the revision (p. 332). *A. u. gracilis* is recognized in the Mexican check-list (Moore, 1957:124).

Cyanocorax unicolor Du Bus 1847 [= *Aphelocoma unicolor unicolor* (Du Bus), p. 420]

The type in the Brussels Museum was examined by me in April, 1958. It is an unsexed adult. My measurements are wing, 169 mm.; tail, 164; bill length, 19.8; tarsus, 43.2. This information supplements that given by van Rossem (1942) and my revision (p. 420).

"*Corvus palliatus* Drapiez," in Bonaparte 1850 [= *Aphelocoma coerulescens californica* (Vigors), p. 389]

Particulars regarding this specimen provided by van Rossem are given in my revision, p. 389. I examined the specimen in the Brussels Museum in April, 1958, and confirmed all those particulars except the following: The specimen is an adult, not a first-year specimen. My wing measurement (119.3) is close to that of van Rossem's (120), but the tail measured 124.0 (not 133). The size characteristics together with weakness of collar pattern suggest a female, probably of the race *californica*, as van Rossem also surmised.

RACIAL TAXONOMY OF APHELOCOMA ULTRAMARINA

The possibility of an additional race of the Mexican Jay from the southern part of the Mexican plateau was considered in my 1951 paper (pp. 346, 419), but this is not supported by additional specimens examined by me since then from Querétaro, Guanajuato, northeastern Jalisco, Aguascalientes, and southern Nayarit (that is, from areas not represented by specimens in my revision; see map page 320).

While the populations on the mountain ranges over the southern part of the plateau, scattered and isolated from each other, are still poorly known (see pp. 316-317), the variation appears to represent merely different degrees of intermediacy between *potosina* to the northeast, *wollweberi* to the northwest and *gracilis* to the west. Also, in spite of the striking size difference between *gracilis* and the race neighboring to the south, *colimae* in western Jalisco, the few specimens I have examined from either side of the Río de Santiago suggest that there are transitional populations between these races.

Specimens from Querétaro in the Museum of Vertebrate Zoology represent *potosina*, and Moore (1957:124) assigns specimens from Guanajuato to that race, also. Those from Aguascalientes and interior Jalisco are best called *wollweberi*. By this usage, the name *wollweberi* is applied to a distinguishable population in the central part of the Sierra Madre Occidental, but included under it are more or less intermediate populations of the southern part of the plateau centrally placed with reference to other, better defined and named populations, but still resembling *wollweberi* most.

In the light of the facts given here along with those given earlier in the discussion of

Garrulus sordidus Swainson 1827, the names of the races of *Aphelocoma ultramarina* should stand as follows:

- Aphelocoma ultramarina ultramarina* (Bonaparte) 1825
- Aphelocoma ultramarina potosina* Nelson 1899
- Aphelocoma ultramarina couchii* (Baird) 1858
- Aphelocoma ultramarina colimae* Nelson 1899
- Aphelocoma ultramarina gracilis* G. S. Miller 1896
- Aphelocoma ultramarina wollweberi* Kaup 1854
- Aphelocoma ultramarina arizonae* (Baird and Ridgway) 1873

A list such as this and the use of trinomials in general often obscures basic speciation problems of continuing interest. One deserves emphasis here. In *Aphelocoma ultramarina*, a major break in the pattern of geographic variation occurs in Hidalgo. There is a large gap in both size and color characteristics between *potosina* and the nominate race (see pp. 321, 340-341). Additional specimens from Hidalgo emphasize this gap, but critical collecting of specimens from localities where the races occur close to each other or even together remains to be done. There is a possibility of circular overlap here between *potosina* and *ultramarina*, the circle being formed by populations to the northwest and west, through *potosina* and *wollweberi*, then to the southwest through *colimae*, then back east through *colimae* and *ultramarina*, or the circle may be smaller in geographic scale. This intriguing possibility is worth investigating notwithstanding the fact that man-induced changes in vegetation and particularly the reduction of forest cover used by Mexican Jays may make the study more than ordinarily difficult.

USE OF SUBGENERA IN APHELOCOMA

The 5th and latest edition of the A.O.U. Check-list (1957) continues the use of subgeneric names *Aphelocoma* and *Sieberocitta* given in the 4th (1931) edition. These were rejected, with explicit reasons, in my monograph, page 420. The chief criterion (Oberholser, 1919) for separation of these subgenera was whether the wing/tail ratio was >1 or <1 . This breaks down and, in fact, broke down prior to the 4th edition, when van Rossem (1928) assigned all forms of the Unicolored Jay to one species, *Aphelocoma unicolor*. Additional criteria originally set forth by Coues (1903:497) also have broken down because the characters either vary intraspecifically (egg patterning in *Aphelocoma ultramarina*; see Pitelka, 1951:317) or never did rank above those of ordinary species differences (color pattern).

Generic limits among the American jays remain uncertain (see Pitelka, 1951:203-206) and need close study by modern standards. As presently delimited, *Aphelocoma* is a compact group of three species hardly calling for use of subgenera. If there is any new evidence or rationale for their use, it should be published if the latest edition of the A.O.U. Check-list is to be taken seriously on this point.

SUMMARY

Types of species and races of the jay genus *Aphelocoma*, not seen in conjunction with a revision of that genus published in 1951, were examined in European museums in 1957-58. These relate to the following names: *Corvus ultramarinus* Bonaparte 1825, *Pica sieberii* Wagler 1827, *Garrulus sordidus* Swainson 1827, *Cyanocitta ultramarinus* Bonaparte 1850, *Aphelocoma wollweberi* Kaup 1854, *Aphelocoma gracilis* G. S. Miller 1896, *Cyanocorax unicolor* Du Bus 1847, "*Corvus palliatus* Drapiez," and *Cyanocitta superciliosa* Strickland 1845.

In the light of new evidence, two changes in trinomial nomenclature are proposed: *Aphelocoma ultramarina potosina* Nelson 1899 is re-applied to Mexican Jays of the

southern part of the Sierra Madre Oriental; and *Aphelocoma coerulescens oocleptica* Swarth 1918 is applied to Scrub Jays not only of the San Francisco Bay region but to all interior Californian populations earlier called *superciliosa* Strickland 1845. The latter name is based on a type specimen not from an interior, but from a coastal population. However, its assignment to a coastal race now cannot be made satisfactorily; without new evidence, it should be considered unusable.

It is proposed additionally, as a result of the change emending *oocleptica* Swarth 1918 and eliminating one racial name, that application of trinomials to racial variation of the Scrub Jay would be more consistent if an additional name be dropped (*cactophila* Huey 1942) since the arguments applicable in the two cases are in part similar. The number of races recognized within the Pacific coast group is thus reduced from ten to eight.

Use of subgenera in *Aphelocoma* as now delimited should be discontinued because all criteria proposed to date are inadequate or invalid.

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TERRITORIAL RELATIONSHIPS BETWEEN CARDINALS AND PYRRHULOXIAS

By PATRICK J. GOULD

The Check-list committee of the American Ornithologists' Union (1957) and Hellmayr (1938) maintain the Cardinal (*Richmondia cardinalis*) and the Pyrrhuloxia (*Pyrrhuloxia sinuata*) in separate genera. However, others (Mayr and Amadon, 1951) have indicated that these two species may be congeneric. The existence of a second species of Cardinal (*Richmondia phoenicea*), which shows tendencies in bill structure toward the Pyrrhuloxia, further suggests the possibility that the two are congeneric. Ridgway (1901) separates the two genera primarily on the basis of bill structure. Although these differences are valid, the question arises as to whether they may be utilized as so-called "generic" characters in this case. Simpson (1945) points out the basic aspect of the genus as a group of similar species. The concept does not regard the genus as a hierarchical category based on one or few character differences but rather as one which stresses groups of similar characters shared by a natural evolutionary group of species. In the absence of paleontological evidence we must rely on similarities displayed by the present day forms. In this respect, ecology and life history are as important considerations as are morphological characters.

Territory in birds has received much attention in recent years. Hinde's (1956) excellent review shows the great differentiation that exists among species which might be used to throw light on relationships. Our best understanding of the value of territory in this connection should come from a comparison of two closely related species which occur together and utilize the same habitat. Several recent studies have been conducted on the relationships between similar species in areas of overlap. These have shown various degrees of relationship depending on the similarity and/or difference between the two species. Lanyon (1957) found in the very similar and closely related meadowlarks that when both species occur in the same area they hold mutually exclusive territories. The two species of towhees studied by Marshall (1960) are separated by more effective isolating mechanisms, and their territories overlap broadly where the two are found together. This paper summarizes the results of a field study on the Cardinal and Pyrrhuloxia in an area where both occur as abundant residents.

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METHODS AND STUDY SITE

A 42-acre area in the San Xavier Indian Reservation, ten miles south of Tucson, Pima County, Arizona, was selected as a study site. This is the same area utilized by Marshall (1960). The site is situated on the first-step lowlands of the Santa Cruz River, and it contains mesquite (*Prosopis juliflora*) woodland with an understory of gray-thorn (*Condalia lycioides*). Elderberry (*Sambucus*) and hackberry (*Celtis*) are common in hedgerows. Much of the mesquite has been cut out and the fields have been cultivated,

but these have been unused for several years. Varieties of weeds, such as Johnson grass and tumbleweed, have overgrown them. Old irrigation pumps and abandoned Indian houses are scattered through the area.

In and around the study site, birds were banded with aluminum bands and with celluloid color bands. Unfortunately the strong bills of the Cardinals and Pyrrhuloxias allowed the birds to bite off many color bands. This resulted in many unmarked birds within the study area. Trapping and banding were continued throughout the study and resulted in the color marking of 38 Cardinals and 84 Pyrrhuloxias. A total of 95 days, with an average of three and one-half hours per day, was spent in the study area from September 30, 1958, to December 18, 1959.

TABLE 1

POSITION OF MARKED BIRDS WITH REGARD TO THEIR SUMMER TERRITORY IN 1959

Male	Number of Observations			
	Outside of territory Sept.-April	May-August	Inside of territory Sept.-April	May-August
C-2	22	2	5	17
C-3	1	1	16	42
P-4	5	1	2	12
P-7	0	0	6	19

Territories were determined primarily by noting the positions of singing males and also the points where fighting and chasing occurred. It was found that nesting began sometime in May and lasted until the middle of August. A tabulation of the points where marked individuals were found during this time was used to verify these territorial boundaries (see table 1). Although territorial establishment began in April, this month has been included in the nonbreeding portion of the annual cycle since territorial boundaries were not perfectly defined at that time.

VOICE

Singing is important in the establishment and maintenance of territory in both the Cardinal and the Pyrrhuloxia. Their songs are so similar that they are often indistinguishable. The major difference in their songs lies in the phrasing used during one singing period. Individuals of both species are capable of a wide variety of song types. In the Cardinal one type is used over and over during one singing period, but the Pyrrhuloxia alternates different types. Although the females of both species are capable of singing, the female Pyrrhuloxia is rarely heard to do so. The female Cardinal, on the other hand, sings loudly and often in duets with her mate, but on only one occasion did I observe a female Cardinal singing without her mate. Duet singing is most common during the spring before nesting begins, but it continues throughout the nesting season and probably aids in the maintenance of the pair bond.

Both species have calls that differ greatly. As soon as the young Cardinals are hatched the adults begin using a high, tinkling call that continues until the young have become independent. The Pyrrhuloxia has a harsh chattering call that is used in territorial disputes and as a contact device between members of a pair.

Songs of both species were heard as early as the second week in February. It was not until the middle of March that singing in both species reached its peak. Since nesting began in May, song probably served in mating and pair formation as well as in establishment of territory. Singing subsided during the latter stages of incubation and was rarely heard after the young were hatched. Singing was renewed after the first brood

became independent if a second brood was attempted. Song in September was reduced to only a few scattered half-songs by one or two individuals.

NESTING

Nest building is apparently carried out primarily by the females of both species. Observations on one Cardinal and one Pyrrhuloxia nest under construction showed only the females building, while the males stayed far back in the trees singing. Most nest material, with only one observed exception, was gathered within the established territory. I never saw material gathered within the territory of another pair.

Nests and nest sites of the species were very similar. Eight Cardinal and 20 Pyrrhuloxia nests ranged between 5 and 15 feet above the ground, both averaging 8 feet. In the study area both preferred to nest either in mesquite or gray-thorn. One nest of the Pyrrhuloxia was found in an elderberry. In other areas around Tucson, Cardinals were found to use tamarisk (*Tamarix*) trees, and Pyrrhuloxia nests were not uncommon in palo verde (*Cercidium*). Both species seemed to prefer thick patches of brush or dense hedgerows; however, of the two species, the Pyrrhuloxia utilized more open situations. Cardinals were much more apt to place their nest against a major trunk of a tree than were Pyrrhuloxias, but both usually placed it in the small twigs that occur on the secondary branches. Neither species anchored the nest securely to the twigs or branch on which it was placed.

The nest of the Cardinal was generally constructed of dead material, although green twigs and stems were sometimes added to the outside. The cup was often poorly lined, and it was composed of only a few rootlets, horse hairs, grass stems, or vine tendrils. The bulk of the nest was composed of thin strips of bark and plant fibers, generally supplemented with grass and soft plant stems. In general the nest was loosely built and eggs could often be seen through the sides and bottom. Several nests were found to contain tissue paper and paper napkins either on the outside or woven into the bulk of the nest.

The nest of the Pyrrhuloxia was almost always constructed of dead material. Of 20 nests only one contained green material, and this amounted to only a few mesquite leaves that had been added to the outside. The nature of the material often gives the nest a very decidedly grayish appearance with brownish highlights. The cup was usually well lined with rootlets, and occasionally thin strips of bark, horse hairs, or very small plant stems and fibers were used. The nest was generally smaller and more compactly built than that of the Cardinal, but the difference was not as great as would be expected from the size difference between the two species.

The eggs of the two species are very similar and cannot always be told apart. In the Tucson area Cardinal eggs are somewhat larger and have a more bluish background color than those of the Pyrrhuloxia. The pattern of speckling is identical. Egg laying may occur any time in the months of May, June, July, and early August (see tables 2 and 3). The most active period for both species was the first two weeks in June. Pairs found nesting in August had probably been unsuccessful in earlier nestings. Clutch size of the Cardinal ranged from two to four eggs and averaged three. Clutch size of the Pyrrhuloxia varied between two and three eggs, both numbers being equally common. In one observed case of each species, incubation required 14 days from the laying of the last egg.

Contrary to the statement by Brandt (1951), Cardinals may have a second brood if their first nesting is successful. Two successful broods were noted in each of two color-marked pairs in the study area. In one case, the second brood was started before the first had become fully independent. I have no information on second nesting in the Pyrrhuloxia.

TABLE 2
NESTING RECORDS OF CARDINALS AT SAN XAVIER RESERVATION IN 1959

Pair no.	Building	Eggs	Nestlings	Fledglings
1				June 17
1			Aug. 8	Aug. 13
2	June 5 destroyed			
2	July 4	July 9 destroyed		
3		June 2 destroyed		
3		July 19 destroyed		
3		Aug. 11 destroyed		
5		June 9	June 11	June 24
5		July 25 (1 egg)	Aug. 11	Aug. 25
6				June 18

Young Cardinals are dependent on their parents for almost a month after leaving the nest. In one case, a color-marked young one first left the nest on August 13 and was still being fed by a color-marked adult on September 5. This may account for the presence of begging young of both species as late as September 30 for Cardinals and September 18 for Pyrrhuloxias.

TERRITORY

Cardinals defend their territories only against trespass by other Cardinals; Pyrrhuloxias defend their areas only against other Pyrrhuloxias. As shown by Hinde (1956), definitions of territory are very numerous. In this paper, territory is defined as that area, within the home range of an individual, which is maintained and defended against members of its own species, and in which the birds sing, nest, raise young, and for the most part restrict their activities. Short excursions are occasionally taken to points outside this area. As seen in table 1, these trips are infrequent and in all instances were made in order to obtain food or water. Territory, therefore, does not include all areas

TABLE 3
NESTING RECORDS OF PYRRHULOXIAS AT SAN XAVIER RESERVATION IN 1959

Pair no.	Building	Eggs	Nestlings	Fledglings
1		July 1 destroyed		
2		June 2	June 9	June 18
3	June 7	June 9 (1 egg)	destroyed	
3	June 24	June 27	July 11	destroyed
3		Aug. 1 (1 egg)	destroyed	
4		June 2 destroyed		
4		June 27	July 4	destroyed
4	July 15	July 19 (1 egg)	destroyed	
7		June 9 destroyed		
7	July 19 destroyed			
8		June 20	?	?
9		Aug. 1	?	?
10				July 29

visited by the birds. Within each territory there is a definite center of activity which is a circular area about the nest. It is here that the birds spend most of their time, especially in the afternoon hours. Here, also, they do most of their singing. Territories are not maintained during the winter. The established adults, however, are always found within a home range which may be much larger than, but always includes, their summer territory.

Of these three types of areas—home range, territory, and center of activity—the territory is the most stable since it is the area most frequently defended. Home range boundaries probably fluctuate greatly and were never observed to be defended. Main-

tenance of a home range helps the birds to become familiar with an area and it also permits individuals to defend the same territory during successive years. One pair of color-marked Cardinals held the same territory in 1960 as they held in 1959. One color-marked male *Pyrrhuloxia* likewise held the same territory for the two consecutive summers.

By the first of September, most of the young have become independent of the adults. Song has almost ceased and no territorial activity can be detected. At this time loose, non-integrated feeding and roosting flocks are formed which contain Cardinals and *Pyrrhuloxias* as well as other species. The *Pyrrhuloxias* always far outnumber the Cardinals in these flocks. This is partly due to the greater number of *Pyrrhuloxias* in the area and partly to the more gregarious habits of the *Pyrrhuloxia*.

The roosting behavior, noted on several occasions, may be indicated by summarizing an observation on November 3. At about sunset, 5:50 p.m., Cardinals and *Pyrrhuloxias* began heading down the hedgerows in large numbers. There was no stopping or back-tracking but rather a rapid series of flights. The great majority of both Cardinals and *Pyrrhuloxias* headed for a section of thick mesquite woodland. There was a lot of calling and moving about in this woodland for approximately five minutes and then everything became quiet for the night.

Establishment.—With the break-up of winter flocks in late February and March, the males of both species became highly pugnacious. This initial activity consisted primarily of individuals chasing each other and it occurred within groups of up to five birds. On April 7 there were five male Cardinals chasing each other in the middle of the study area. No direct conflicts were noticed, but this aggressiveness was in sharp contrast to their winter tolerance. Later in the summer four of these males established territories within the study area, and the point of chasing of April 7 became a boundary between three of their territories. Female *Pyrrhuloxias*, but never female Cardinals, were noticed to engage in chasing activities, often with the males. These chases apparently establish a dominance order between the individuals so that the most aggressive male succeeds in taking the best territory. This was exemplified by Cardinal male number 3. He was the most vigorous bird in fighting and chasing, and he was most often observed to be the aggressor. He was the first male to completely establish a territory, and this territory contained the best nesting sites and food supply within the study area.

During late April and early May definite territorial boundaries became established. As in the early stages of this process, only the male Cardinal, but both the male and female *Pyrrhuloxia* were involved. On one occasion a pair of *Pyrrhuloxias* was noticed moving about an area which eventually became their territory. At one point another pair was encountered and all four birds engaged in a vigorous fight. The intruding pair was driven out and was never noticed to encroach on that area again.

Maintenance.—Territories once established were maintained almost entirely by the males of both species. The female assisted in defense only when the nest or young were threatened directly. At times she did not even do this but flew off and left defense completely to the male. In every instance when a Cardinal nest with eggs was being examined, the adults would skulk in the background occasionally uttering high, sharp chips. When young were in the nest, both parents, but more noticeably the male, would hop around excitedly, often quite close to the observer, using the high, tinkling call previously described. When a *Pyrrhuloxia* nest and eggs were examined the female completely disappeared, but the male often stayed in the same tree and sang vigorously. If young were in the nest, the male, and sometimes the female, would fly around excitedly singing or giving their chatter call.

Territory was maintained in three primary ways: combat, proclamation, and patrolling. Combat, which includes both fighting and chasing, was noticed in both species, but it was much more vigorous in the Pyrrhuloxia. An intruding bird would be met, usually near the boundaries of the territory and either a fight or a chase, and often both, would follow. In all cases the intruder was forced to leave the area. If contact was made well within the territory, the intruder was much more prone to take flight, resulting in a chase. If contact was made near the boundary, then a fight was more likely to occur. For the most part, intrusions were made only by males of adjoining territories. Unmated birds passing through the area were generally tolerated, but an established bird never was. On July 1 an unbanded Cardinal was noticed singing at the northwest boundary of the territory of Cardinal number 1. The latter came up close to the singing male and chipped several times, but no fight ensued. Since this unbanded male was never found to be singing in this area again, it is presumed that he was an unmated bird just passing through the area.

Proclamation of territory consisted of intensive singing on the part of the males of both species. It was most frequent during the early morning, when a chorus of many birds could be heard. At this time singing would usually be from a favored site within the center of activity of the territory. Occasionally during the day competitive singing between males of the same species was heard. This was equally common in the Cardinals and Pyrrhuloxias. The males sang either in unison or alternated with each other. This type of song was most common between males of adjoining territories. Competitive singing between widely separated males was heard on only a few occasions.

Patrolling was noted in both species; however, only the Pyrrhuloxia followed a regular pattern. Cardinals merely wandered irregularly about their territories, singing in many scattered places. Cardinal male 1, for example, sang at scattered spots within his territory throughout the day. His singing on the boundaries of his territory was just as irregular. Some days he would be found singing at the south boundary and then on other days he sang on the northwest boundary. The same trees are used for singing quite frequently through the summer and these points were utilized in delimiting his territory. His flight patterns to and from these singing posts were very regular, and this offered further proof of his territorial limits. All the other male Cardinals in the study area followed the same pattern. The Pyrrhuloxia, as exemplified by male number 7, made a regular circuit of his territorial boundary. After the initial singing in the morning the male would make his rounds, singing a few songs in one bush and then in the next, until a complete circuit had been made. He was never observed outside of the area just described.

Once the young are out of the nest, territorial defense and maintenance were reduced, and they stopped entirely if it was late in the season. If a nest was destroyed, territorial activity increased although it never reached the peak of the initial activity. Individual pairs of both species were seen to make as many as three attempts at reneating, with a recurrence of high territorial activity, if their nests were abandoned or destroyed.

Composition.—Within the limits of the study area, territories of six Cardinals and ten Pyrrhuloxias were established (see figs. 1, 2). The total portion of the study area occupied by Cardinals was 54.5 per cent, whereas that occupied by the Pyrrhuloxias was 60 per cent. Both species required a suitable amount of woodland within each territory. An average of 45 per cent of the territory of each pair of Cardinals and 43 per cent of the territory of each pair of Pyrrhuloxias included mesquite woodland (see table 4). Cardinals appeared to require denser woodland in which to nest than did Pyrrhuloxias. An example of this was the fact that, although Cardinals were occasionally

seen and heard to sing from an open mesquite patch, none established a territory there. One pair of Pyrrhuloxias (pair 2), however, was able to establish a territory at this spot and raise one family. This patch consisted of small and widely spaced mesquite trees with much open, weed-covered ground between them. In other areas near Tucson, Car-

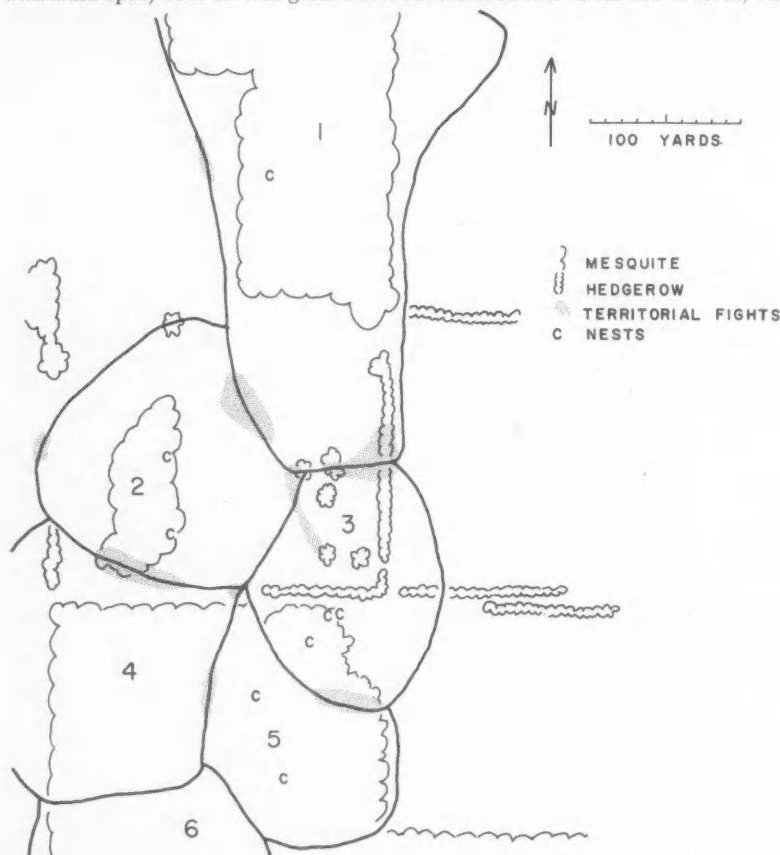


Fig. 1. Diagram showing six territories of Cardinals (*Richmondia cardinalis*) within the study area.

dinals were found nesting in hedgerows between open fields, but these were always fairly dense and contained large trees. In these same areas the Pyrrhuloxias were often found nesting in trees with little or no vegetation around them.

Both Cardinals and Pyrrhuloxias appear to prefer an open field within the limits of their territory. This is not too surprising because, as shown by McAtee (1908), their diet consists of weed seeds. The fact that one territory did not include such an area shows that this is not absolutely necessary. Food supply apparently plays only a minor role in the territorialism of these birds, but this paper offers no direct evidence on this

long-debated point. Even though most territories included a considerable area of open fields, these fields were not exploited to their maximum. Often birds of both species were seen feeding together in groups outside of their territories. No conflicts were noticed on these occasions, indicating that these feeding areas were not part of established terri-

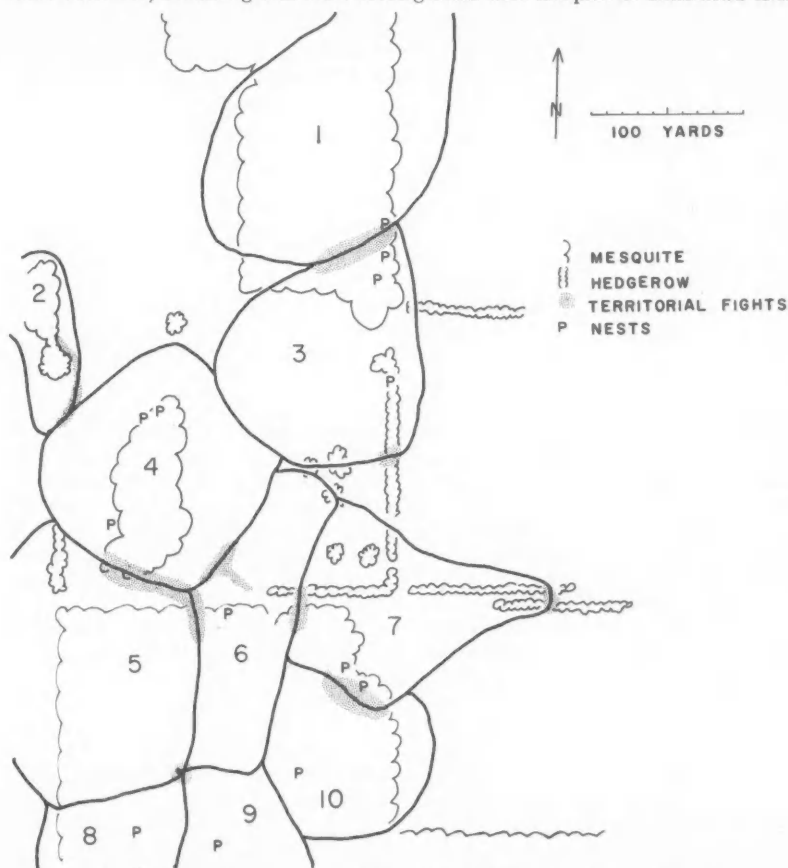


Fig. 2. Diagram showing ten territories of Pyrrhuloxias (*Pyrrhuloxia sinuata*) within the study area.

tories. During the height of the breeding season, two color-marked Cardinals (numbers 2 and 3) were seen fighting near the border of the territory of one of them. A chase ensued and continued to the boundary between their respective territories. At this point the chase stopped and both birds fed within a foot of each other. Although this may have been an example of "substitute activity" (Tinbergen, 1939), it is thought by the author that if food were of major importance in territoriality, the mere act of feeding in close proximity, regardless of the cause, would have aroused aggressive behavior rather than suppressing or displacing it.

Size and shape.—The size of the territories within the study area is given in table 4. Territorial fights of Cardinals and Pyrrhuloxias are summarized in figures 1 and 2. Other disputes that were not as well documented are not included. It will be seen from these figures that the territorial boundaries are not thin lines but often bands of perhaps five or ten yards in width. In these areas the boundary lines are drawn through the area where the fighting was most intense or along the major flight path during the chasing. Two territorial fights between Cardinals 2 and 4, and one between Pyrrhuloxias

TABLE 4
SIZE OF TERRITORIES AND AMOUNT OF MESQUITE WOODLAND WITHIN EACH

Cardinal			Pyrrhuloxia		
Pair no.	Territory	Per cent of mesquite	Pair no.	Territory	Per cent of mesquite
2	3.9 acres	19	2	1.3 acres	27
3	3.9	16	3	2.9	25
4	4.1	51	4	3.5	50
5	3.5	94	5	3.3	52
			6	2.2	54
			7	2.2	18
			10	2.3	78
Average	3.7 acres	45	Average	2.5 acres	43

4 and 5, were almost identical with regard to the place where fighting was most intense and as to the pattern of the chase. In all three cases it was the northernmost male who chased the other male in a southeastern arc. Similarly the fights between Cardinals 3 and 5, and Pyrrhuloxias 7 and 10, were almost identical.

The shape of the territories of both species tended to be roughly circular. They were, however, modified by the landscaping and other factors. Territories were modified, where possible, to cover both mesquite woodland and open fields. Hedgerows afforded greater penetration into open areas by providing trees and bushes from which advertisement could be made. Pyrrhuloxia territory number 7 was an example of this. Pyrrhuloxia territory number 6 was very compressed by the other territories around it. This resulted in a long, thin territory which included both mesquite woodland and an open field.

The size, shape, and position of territories of Cardinals and Pyrrhuloxias were remarkably similar. This was so striking that if a person viewing the maps of them were not aware that two species were involved, he might think they represented the same species during different breeding seasons. The similarity is even more striking when these territories are compared with the dissimilar territories of Brown and Abert towhees as described by Marshall (1960) from the same area. Such differences as exist between territories of Cardinals and Pyrrhuloxias are due to the greater number of Pyrrhuloxias in the area. For example, Cardinal territory 1 was roughly equivalent to Pyrrhuloxia territory 1 plus 3. Territories of Cardinal 2 and Pyrrhuloxia 4 were almost identical, as were those of Cardinal 3 and Pyrrhuloxia 7. Pyrrhuloxia number 6 was squeezed in between many others as shown by the greater number of territorial fights engaged in by this pair. In the study area, the ratio of number of territories of Cardinals to territories of Pyrrhuloxias was 1 to 1.6. The ratio of territory size was 1.5 to 1. Results of netting and trapping, which were not selectively different between the two species, showed that the Pyrrhuloxias outnumbered the Cardinals in the area by about 2 to 1. Therefore, the differences in size and shape between territories of Cardinals and Pyrrhuloxias was due to the greater density of the Pyrrhuloxias.

The size and shape of the territories remained fairly stable during the summer.

However, a few minor fluctuations were noted. These were primarily the result of the shifting of the center of activity when a new nest was built. If the new nest was built on the opposite end of the territory from the old one, then the region of the old nest was not defended as often nor as vigorously as before. This allowed a neighboring pair to gain control of the vacated area. The nest of Pyrrhuloxia 1 was destroyed and this pair moved farther north. When the nest of pair 3 was destroyed, they re-nested near the boundary of the territory of pair 1. Several fights between these two pairs occurred at this time. No further fights occurred after the initial few and pair 3 successfully held part of the territory of pair 1 for the rest of the summer.

Nest sites were placed without regard to the size or shape of the territory. Some were in the middle and others were at the edge (see figs. 1, 2). Similarly there was much randomness with regard to placement in relation to the mesquite woodland, although Cardinals did not nest in hedgerows as did a few pairs of Pyrrhuloxias. Cardinals and Pyrrhuloxias tended not to nest near each other. The fact, however, that Cardinal 5 and Pyrrhuloxia 6 had concurrent nests only three yards apart, shows that proximity may not be critical. Since both species utilize the same type of place to build the nest, and since the nests and eggs are so similar, this tendency not to nest near each other may be a result of some form of competition.

SUMMARY AND CONCLUSIONS

Territorial behavior and other aspects of the life of the Cardinal and the Pyrrhuloxia in southern Arizona are basically very similar. Their songs are homologous and at times they are indistinguishable. These songs are of prime importance in the establishment and maintenance of territories. They may also aid in pair formation, but only in the Cardinal are they involved in a definite ritualistic duet, which strengthens the pair bond. The female Pyrrhuloxia is rarely heard in the field. A second type of vocalization is present in both species, but these calls are not homologous. Both species begin singing in the middle of February, and by September, singing is almost nonexistent.

The nesting cycle and habits are almost identical. Such differences as smaller egg- and nest-size of the Pyrrhuloxia are most likely a function of its smaller body size. The ability of the Pyrrhuloxia to nest in more open situations suggests a mechanism for reducing competition between the two species.

The territories of these two species are not mutually exclusive. On the contrary, they are often coincident. This suggests that the difference in the average size and in the shape of their territories is a function of local density. Food supply is considered of only minor importance in the territorialism of these birds.

The size, shape, and position of territories, along with the almost identical amount of woodland within each, and the basic similarities in the breeding behavior and cycle, suggest that the ecological requirements of these two species are extremely similar. Differences in ecology which cause a different geographic distribution of the two are not evident on the study area, where they both occur and utilize the same environment in the same way. The considerable similarity between the two species in life history supports the hypothesis that they are congeneric.

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BIRDS OBSERVED DURING TWO CROSSINGS OF THE PACIFIC OCEAN

By DANIEL C. WILHOFT

Several recent papers have dealt with the distribution of pelagic birds in one or more areas of the Pacific Ocean. Yocom (1947) reported on birds from four oceanic stations in the North Pacific. Thompson (1951) added valuable data on the Black-footed Albatross (*Diomedea nigripes*) observed between San Francisco and Hawaii. Arnold (1948), Kuroda (1955), and Hamilton (1958) reported general observations and gave data on the Black-footed Albatross in several areas of the North Pacific. Dixon and Starrett (1952) published observations on seabirds of the Western Pacific Ocean and King and Pyle (1957) discussed observations made in the South Pacific.

In July, 1959, I crossed the Pacific Ocean on a passenger ship enroute to Australia. A return trip was made between August 3 and September 3, 1960. The courses of the crossings are shown in figure 1. Both ships maintained an average speed of 22 knots. A total of 36 days of observations at sea was possible. Table 1 lists the daily noon position of the ships, the air and water temperatures, humidity, and approximate wave height. Observations were carried out from the upper boat deck astern. From this vantage point, approximately 80 feet above the ocean surface, the sky overhead and astern plus both port and starboard beams could be observed by walking a few feet to either rail. Four hours of observations with 7×50 binoculars were conducted daily during the following periods: 7:00 to 8:00 a.m., 11:00 a.m. to noon, and 4:00 to 6:00 p.m. In addition the boat deck was checked almost every night for any birds that might have settled thereon after having been attracted by the ship's lights. No such birds were found. The numbers of individuals observed and identified are listed in the species accounts. All figures represent accumulated daily totals.

On the basis of water masses and currents the Pacific Ocean can be divided into the following regions: North Pacific with Subarctic, Western Central and Eastern Central water masses and the Kuroshio, Northern Pacific, Subarctic and California currents; Equatorial region with a single water mass of remarkably uniform character and North Equatorial and South Equatorial currents, and Equatorial Counter-current; South Pacific with the Subantarctic, western South Pacific and eastern South Pacific water masses and the poorly understood Perú Current (Sverdrup, Johnson, and Fleming, 1942). With the possible exception of the eastern South Pacific Water Mass all the areas just mentioned were transited.

I wish to express my appreciation to Dr. William J. Hamilton, III, for suggesting that I undertake these observations and to members of the engineering departments of the S.S. Oronsay and S.S. Himalaya who kindly supplied various data. Also I wish to thank Mr. Richard Banks and Dr. Seth B. Benson for reading the manuscript and offering helpful suggestions. The trip was made possible through a Fulbright Grant for which I am sincerely grateful.

ANNOTATED LIST OF SPECIES

The following species of birds were observed and recorded during the 36 days spent at sea. Peters (1931-1934) has been followed in respect to scientific names and order of listing. Common names are as given in Alexander (1954).

Diomedea exulans. Wandering Albatross. This species was observed on three occasions on the voyage in 1959 and not at all in 1960. It was observed only in the vicinity of New Zealand, either on the day preceding our entry to Auckland Harbor or the two days following our departure. On all but the last day two other species of albatrosses (Light-mantled Sooty and Black-browed) and many

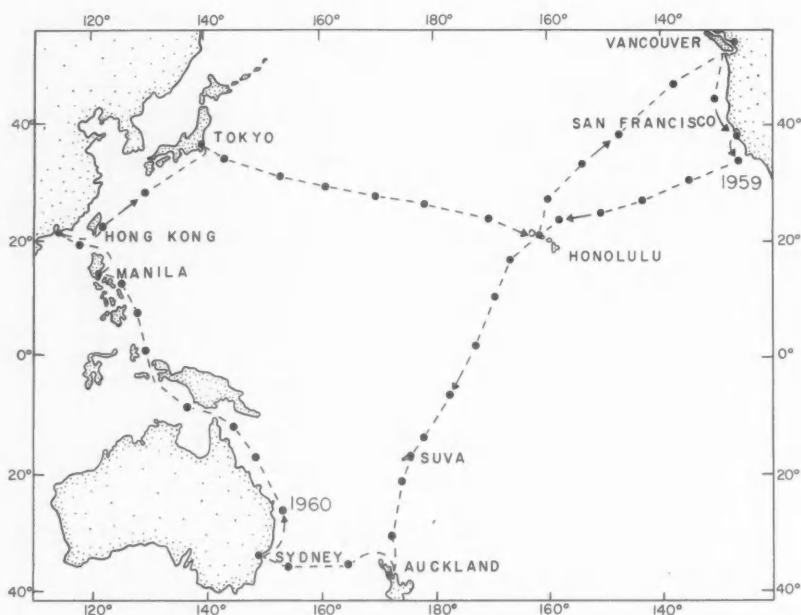


Fig. 1. Daily positions of ship during two crossings of the Pacific Ocean. The ports of Los Angeles and Kobe are not included in the figure.

unidentified petrels were also observed. July 28, 1959, $31^{\circ} 24' S$, $175^{\circ} 46' E$, 6 birds; July 30, 1959, $34^{\circ} 14' S$, $168^{\circ} 45' E$, 6 birds; July 31, 1959, $34^{\circ} 04' S$, $158^{\circ} 16' E$, 3 birds.

Diomedea nigripes. Black-footed Albatross. The occurrence of nonbreeding concentrations and factors influencing such concentrations of this species has interested several writers. Miller (1940), in the course of systematic cruises in the waters off the southern California coast found concentrations of Black-footed Albatrosses in waters which were relatively cold, turbulent, and rich in nutrients and zooplankton. Thompson (1951) found higher concentrations of birds following his ship in the cooler waters of the California Current than in the warmer waters to the west. He concurs with Miller that concentrations of birds appear greater in waters of relatively low temperature. It is assumed here that it is not the water temperature itself which is influencing the distribution of albatrosses but rather the apparent higher concentrations of food in the relatively cooler waters. Farther north Yocom (1947) found a more constant distribution in both warm and cold waters. Kuroda (1955) found the greatest number of this species in the warmest waters he encountered (see table 2), although his "warmest" is only $14^{\circ}C$. Hamilton (1958:161) reports: "Further, the abundance of this species in the warm (14° – $17^{\circ}C$.) waters off Japan suggests that concentrations are not actually confined to waters of low temperature."

Because of the previous interest in this species the writer was especially alert in observing it. Noted beyond are dates, localities, water temperature, and numbers of birds observed. Table 2 is a comparison of numbers of birds seen in waters of different temperatures as recorded by Kuroda, Hamilton and myself.

The large concentration observed on August 11, 1960, was farther south than one might expect, especially for the time of year, although Cogswell (1946) reported observing this species in the vicinity of Johnson Island ($18^{\circ} N$ latitude) in the month of April, and Swinhoe (1863) reported these albatrosses as being common throughout the year in the Formosa Channel ($25^{\circ} N$ latitude). Tem-

TABLE 1

NOON POSITIONS OF SHIP AND AIR AND WATER TEMPERATURES ENCOUNTERED
IN CROSSING PACIFIC OCEAN

		Noon position Latitude	Longitude	Air temp. °C.	Water temp. °C.	Humidity per cent	Waves (height)
1959							
July	13	35° 40' N	121° 05' W	13.0	14.5	4-6 ft.
	14	Port					
	15	32° 52' N	122° 38' W	16.0	17.0	80	3-4
	16	30° 50' N	132° 34' W	18.0	20.0	80	3-4
	17	27° 58' N	142° 11' W	22.0	22.0	72	1-2
	18	24° 24' N	151° 01' W	26.0	25.0	64	1-2
	19	Port					
	20	17° 44' N	159° 56' W	28.0	26.5	72	3-4
	21	10° 08' N	164° 40' W	27.5	28.5	88	3-4
	22	02° 32' N	168° 52' W	27.5	28.5	92	1-2
	23	05° 33' S	173° 11' W	27.5	29.0	72	1-2
	24	13° 37' S	177° 18' W	29.0	29.0	78	1-2
	25	Lost this day by crossing International Date Line					
	26	Port					
	27	23° 47' S	177° 04' E	20.0	22.0	86	1-2
	28	31° 24' S	175° 46' E	20.0	19.0	76	1-2
	29	Port					
	30	34° 14' S	168° 45' E	14.5	17.0	90	2-4
	31	34° 04' S	158° 16' E	14.5	20.0	96	2-4
1960							
Aug.	3	27° 20' S	153° 30' E	15.5	22.5	56	2-4
	4	19° 47' S	148° 17' E	20.5	22.5	45	1-2
	5	13° 22' S	143° 40' E	23.0	26.5	60	1-2
	6	09° 20' S	137° 07' E	22.5	29.0	80	1-2
	7	04° 51' S	129° 21' E	29.0	29.0	85	1-2
	8	02° 51' N	124° 48' E	30.0	29.0	87	1-2
	9	10° 06' N	121° 45' E	30.5	30.0	86	1-2
	10	Port					
	11	16° 05' N	119° 02' E	29.5	30.0	83	3-4
	12	Port					
	13	Port					
	14	Port					
	15	22° 05' N	121° 22' E	27.5	29.0	85	1-2
	16	27° 22' N	129° 13' E	27.5	27.5	82	3-4
	17	Port					
	18	34° 25' N	139° 15' E	25.0	27.5	65	1-2
	19	Port					
	20	Port					
	21	34° 09' N	146° 29' E	24.5	26.5	92	Typhoon
	22	34° 56' N	157° 00' E	24.5	25.5	78	3-4
	23	33° 36' N	168° 14' E	25.0	25.5	50	1-2
	24 E	30° 35' N	178° 15' E	25.5	26.5	82	1-2
	24 W	27° 19' N	172° 25' W	25.0	27.5	90	1-2
	25	24° 21' N	163° 30' W	25.5	27.5	82	1-2
	26	Port					
	27	25° 10' N	154° 48' W	25.0	26.5	75	1-2
	28	30° 47' N	148° 15' W	24.5	24.5	73	1-2
	29	37° 19' N	140° 19' W	22.0	24.5	74	1-2
	30	43° 32' N	132° 21' W	16.0	25.5	80	1-2
	31	Port					
Sept.	1	Port					
	2	44° 15' N	126° 01' W	15.0	20.0	75	1-2

All readings were taken at noon each day with the exception of the sea water temperature which was obtained at 8:00 a.m.

porary climatic conditions might have had considerable influence on the position of these birds, as there had been two severe typhoons between Japan and Formosa just before my observations.

The data reported here would support Hamilton's contention that concentrations are not actually confined to waters of low temperature at least during the summer months. As he further pointed out, extensive observations, a better knowledge of the food habits of this species, and data on the abundance of food in various bodies of water are essential before any final determination can be made of the cause of such concentrations.

Date	Locality		Number	Water temperature
1959				
July 13	35° 40' N	121° 05' W	6	14.5°C.
July 15	32° 52' N	122° 38' W	2	17.0°C.
July 16	30° 50' N	132° 34' W	31	20.0°C.
July 17	27° 58' N	142° 11' W	1	22.0°C.
1960				
August 11	16° 05' N	119° 02' E	70+	30.0°C.
August 22	34° 56' N	157° 00' E	3	25.5°C.
August 25	24° 21' N	163° 30' W	50+	27.5°C.
August 29	37° 19' N	140° 19' W	13	24.5°C.
August 30	43° 32' N	132° 21' W	15	22.5°C.
September 2	44° 15' N	126° 01' W	9	20.0°C.

Diomedea immutabilis. Laysan Albatross. Only one individual was observed; it flew along the starboard side of the ship for about 5 minutes and then flew back over the wake in rather characteristic albatross manner. August 22, 1960, 34° 56' N, 157° 00' E.

Diomedea melanophris. Black-browed Albatross. Three of this species were observed in the afternoon one day before entering Auckland Harbor. Two other species of albatrosses (Light-mantled Sooty and Wandering) were observed early in the afternoon, but by 4:00 p.m. only two of the Black-browed Albatrosses were still foraging in the wake of the ship. Several small black and white petrels were also observed, but no positive identification could be made. July 28, 1959, 31° 24' S, 175° 46' E.

TABLE 2

NUMBER OF BLACK-FOOTED ALBATROSSES OBSERVED AND TEMPERATURE OF SEA WATER IN THE NORTH AND CENTRAL PACIFIC IN JUNE, JULY, AND AUGUST*

Temperature °C.	Numbers			
	Kuroda	Hamilton	Wilhoft	Total
0-1
2-3	0
4-5	3	3
6-7	2	2
8-9	3	3	6
10-11	10	48	58
12-13	17	3	20
14-15	0	15	5	20
16-17	11	14	2	27
18-19	0	0	0
20-21	25	12	37
22-23	16	16
24-25	6	6
26-27	50+	50+
28-29	70+	70+
30-31

* Compiled from Kuroda (1955), Hamilton (1958) and Wilhoft. Dots (....) signify temperatures not encountered during observations.

Diomedea cauta. Shy Albatross. Three of these albatrosses were observed in the Tasman Sea together with 6 either female or immature Wandering Albatrosses. July 30, 1959, 34° 14' S, 168° 45' E.

Phoebastria palpebrata. Light-mantled Sooty Albatross. Six of this species were observed on two occasions, each only one day out of Auckland Harbor. It is interesting to note that the two previously recorded species plus the Wandering Albatross were only observed in the immediate vicinity of New Zealand and not farther out at sea. July 28, 1959, 31° 24' S, 174° 46' E, 4 birds; July 30, 1959, 34° 14' S, 168° 45' E, 2 birds.

Puffinus leucomelas. White-faced Shearwater. The day before entering Yokohama Harbor several hundred shearwaters and petrels were observed. Of these birds, 22 were positively identified as White-faced Shearwaters. The others were too far off for positive identification. August 18, 1960, 34° 25' N, 139° 15' E.

Pterodroma phaeopygia. Hawaiian Petrel. For three days (two days before entering Honolulu and one after) these petrels were very numerous. On the first day they were sighted, only three were observed during each of the first two observation periods (7:00 and 11:00 a.m.), but by 4:00 p.m. there were at least fifty birds around the ship. On the second day they were numerous between 11:00 a.m. and noon. Only one was sighted before this hour, even though observations were continuous from 7:00 a.m. By 4:00 p.m. there were literally thousands of them in the vicinity. They appeared to be in groups of a few hundred and as the ship approached, the entire group would lift off the water and fly away from the ship. During this period observations were made from the bow rather than from the stern. On the morning of August 27, when we were east of the Hawaiian Islands, only six petrels were observed and none after this day. I can offer no explanation for the large numbers of these birds to the west of the Hawaiian Island chain and the relatively few to the east. August 24, 1960, 27° 19' N, 172° 25' W, 60+ birds; August 25, 1960, 24° 21' N, 163° 30' W, 2000+ birds; August 27, 1960, 25° 10' N, 154° 48' W, 6 birds.

Phaethon rubicauda. Red-tailed Tropic Bird. This spectacular species was observed on three occasions. On the first and second observation only one individual was seen and on neither occasion did the bird remain in close proximity to the ship for very long. Tropic birds seemed to be curious and would fly over the stern rather low looking at the deck and then fall astern of the ship. During the third observation six of these birds were seen early (7:00 a.m.) in the morning and continued to follow the ship closely for the day. They came very near to the stern and on several occasions flew over the bridge. July 20, 1959, 17° 44' N, 159° 56' W, 1 bird; July 24, 1959, 13° 37' S, 177° 18' W, 1 bird; August 24, 1960, 27° 19' N, 172° 25' W, 6 birds.

Sula dactylatra. Blue-faced Booby. These birds were observed on seven different occasions in the course of the two crossings. Often they would fly close to the ship, apparently curious about it. Although on at least one occasion (August 7, 1960) these birds were seen simultaneously with flying fish, there was no indication of predatory behavior on the part of the boobies. The last two observations of these birds were made somewhat far north for this species, but the typhoons mentioned previously plus a third off the coast of Japan on August 21, just three days previous to these observations, might account for the birds' rather northerly position.

Date	Locality	Number
July 20, 1959	17° 44' N 159° 56' W	1
July 24, 1959	23° 47' S 177° 04' E	2
August 4, 1960	19° 47' S 148° 17' E	18
August 7, 1960	04° 51' S 129° 21' E	12
August 9, 1960	10° 06' S 121° 45' E	69
August 24, 1960	30° 35' N 178° 15' E	1
August 25, 1960	24° 21' N 163° 30' W	11

Sula leucogaster. Brown Booby. Although more individuals of this species were observed than of *S. dactylatra*, they were not as frequently encountered. They were seen on only three occasions and then reasonably close to land. On the two days in 1959 when they were numerous we were in close proximity to small islands situated northeast of Fiji. Likewise in 1960 when these birds were observed, we were close to land passing through the Manipa Straits. At this location they occurred with *S. dactylatra*. On one occasion (August 7, 1960) a booby was observed to dive into the water from a height

of approximately fifty feet, but nothing was seen in its bill when it reappeared. July 23, 1959, 05° 33' S, 173° 11' W, 100+ birds; July 24, 1959, 13° 37' S, 177° 18' W, 50+ birds; August 7, 1960, 04° 51' S, 129° 21' E, 12 birds.

Fregata minor. Great Frigate Bird. Four of these birds were observed on the trip. Three of them were seen when we were only a day out of Honolulu. On each occasion they hovered over the stern of the ship for a few minutes. They appeared to be rather curious and once having looked over the ship they glided away. July 18, 1959, 24° 24' N, 151° 01' W, 1 bird; August 9, 1960, 10° 06' N, 121° 45' E, 1 bird; August 25, 1960, 24° 21' N, 163° 30' W, 2 birds.

Larus novaehollandiae. Silver Gull. Of the several types of gulls that were observed in harbors, the Silver Gull was the only species also observed at sea. It should be pointed out that the last two observations here recorded were made while we were passing between the Great Barrier Reef and the eastern coast of Australia. August 4, 1960, 19° 47' S, 148° 40' E, 24 birds; August 5, 1960, 13° 22' S, 143° 40' E, 50+ birds; August 6, 1960, 09° 20' S, 137° 07' E, 40+ birds.

SUMMARY

Birds observed in the course of 36 days at sea in the Pacific Ocean between San Francisco and Australia, Australia and Japan, and Japan and San Francisco are recorded. The correlation of water temperature with the occurrence of nonbreeding concentrations of Black-footed Albatrosses is compared with results of two other workers. Based on this comparison it is suggested that such concentrations occur in a wide range of water temperatures, from 11° to 29°C. More extensive observations, plus a more precise knowledge of feeding habits of this albatross are needed before final determinations can be made of the causes of concentrations.

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Museum of Vertebrate Zoology, Berkeley, California, December 18, 1960.

FROM FIELD AND STUDY

Egg Sizes of Laysan and Black-footed Albatrosses.—As one phase of a research program on the albatrosses of Midway Island, in October, November, and December, 1958, a study was made of the eggs of these birds. This work was supported by a contract between the Office of Naval Research, Department of the United States Navy, and the Pennsylvania State University, NR 160-464.

The Laysan Albatrosses (*Diomedea immutabilis*) and Black-footed Albatrosses (*Diomedea nigripes*) arrive at Midway in November to mate and nest. Eggs were easily obtained by moving the docile parents from the nests and substituting a deserted egg. The birds immediately started brooding the substitute egg, and measurements of the borrowed egg were made. Some eggs from nests where the parents had accidentally died were also measured. The eggs of the Black-foots were studied on December 3 and 4 and had been incubated for about 3 weeks. The eggs of Laysans were studied from December 8 to 10 and had been incubated about 2 weeks. About 100 females of each species were dissected to study the eggs in the oviduct.

The length of an egg was measured with outside-measuring, wood-working calipers and a ruler. The diameter at the largest part was measured with a pair of long-jaw calipers. Weights were taken with a triple-beam balance. Volumes were measured by a water-displacement method: an egg was placed in a container of known volume and water added until the container was full; the amount of water was then measured and subtracted from the total volume of the container.

The results are given in table 1. Eggs of Black-foots seem to be slightly larger on the whole than eggs of Laysans. This may be a result of the difference in size between the two species, the Black-foots being slightly larger birds. The results correspond favorably with those of Richards (Condor, 11, 1909:122-123) and Bent (U.S. Nat. Mus. Bull. No. 121, 1922), who used relatively few eggs. An exception, however, occurs in the diameters, where the correspondence is only fair. There is considerable variation in size and proportions of the eggs. Some are almost round, whereas others are elongate; some have the greatest diameter close to one end, and others have it almost in the middle.

TABLE 1

MEASUREMENTS AND WEIGHTS OF EGGS OF 20 LAYSAN AND 100 BLACK-FOOTED ALBATROSSSES,
AND VOLUMES OF EGGS OF 14 LAYSAN AND 50 BLACK-FOOTED ALBATROSSSES

	Lengths (mm.)		Diameters (mm.)	
	Mean±S.E.	Range	Mean±S.E.	Range
Laysan	107.6±0.80	101-113	75.0±0.46	71.1-77.9
Black-foots	107.1±0.43	97-121	76.2±0.25	67.6-81.0
	Weights (gm.)		Volumes (cc.)	
	Mean±S.E.	Range	Mean±S.E.	Range
Laysan	278.5±4.8	240.5-326.1	265.1±6.0	234.5-305
Black-foots	291.0±2.3	218.5-334.7	272.3±3.6	196-313

S. E. = Standard error of mean; range = observed range.

The eggs are creamy white with brown spotting. There is a pronounced cap of reddish brown on the larger end of the majority of the eggs. The cap varies greatly in size and shape, as do the spots; some of the eggs are almost entirely white, whereas others are almost all brown. The brown color is due to blood from the oviduct which dries after the egg is laid. At the time when the egg shell is formed in the proximal part of the oviduct, there are no markings. As the egg passes down the oviduct, small hemorrhages almost always occur, and blood comes in contact with the egg. The dark cap at the large end is produced as the egg is laid. Sometimes small pieces of coral sand adhere to the egg as it is laid and become an integral part of the shell, giving it a rough appearance.

Egg laying is an interesting procedure. It is easy to tell when a female is ready to lay an egg; she stands over the nest with her wings drooping at her sides and looks under herself. She dips her tail toward the nest at intervals, accompanying this with squeaks and groans. Suddenly the egg appears in the nest after one of her tail dips. The female stands a moment and then sits down on the egg. Usually shortly afterward, the male replaces the female on the nest and assumes the first responsibility for incubation.—CARL FRINGS, *State College, Pennsylvania, November 15, 1960.*

Western Grebe Colonies in Northern Colorado.—The Western Grebe (*Aechmophorus occidentalis*) was noted by Sclater (History of the Birds of Colorado, 1912:4) only as a rare fall migrant in Colorado. In 1940, however, Bailey and Brandenburg (Condor, 43, 1941:73) observed a nesting colony of Western Grebes in the San Luis Valley of southern Colorado. This species has now become one of the most common breeding birds on the larger reservoirs of the irrigated plains just east of the foothills in northern Colorado. This fact, which is well known to local bird students, seems not to have been recorded in the literature.

I first saw Western Grebes (three individuals) on June 11, 1953, at Terry Lake, a shallow, 1½-mile-long reservoir just north of Fort Collins at about 5000 feet elevation. It is likely that they were already breeding in the area at that time. Later, from 1957 to 1959, I made ten observations at six separate nesting colonies on this and three similar reservoirs, all between 4900 and 5000 feet elevation. The other localities involved are: Timnath Reservoir, 1½ miles long; Fossil Creek Reservoir, 2½ miles long; and Boyd Lake, 3½ miles long. These are situated about five miles east-southeast, six miles south-southeast, and eight miles south of Fort Collins, respectively. All these reservoirs are partly, but not predominantly, fringed with cottonwood and willow trees; the establishment of cattails and other marsh vegetation is prevented by fluctuation of the water level, except in small patches a few rods to a few acres in extent, where there is ground water seepage. The grebes nest only in years when the water is high enough to flood these marsh areas or marginal zones of tall weeds or brush on the otherwise exposed shores. From 1957 to 1959 these reservoirs remained at their highest possible levels all through the early summer, and the grebes found conditions favorable for nesting in water one to four feet deep near the shore. Water two to three feet deep was preferred.

Surprising versatility in choice of nest sites was shown. In a 16-nest colony found at the north-west end of Terry Lake on May 26, 1957, only one egg had been laid. At this site there was a partly submerged patch of bulrushes, but the grebes had used it only as a source of nest material, mooring the nests in scattered willow bushes at the edge of open water. On June 9 of the following year there were 13 nests in the same area.

On June 8, 1957, laying was under way in two colonies, several hundred feet apart, at the north-east corner of Timnath Reservoir. The westernmost colony included about ten occupied nests in an exposed situation in a very thin growth of dead, half-submerged *Kochia* and cockleburrs about 100 feet from shore. The other was in the outer edge of a patch of bulrushes and included five nests, only one of which contained eggs. Nesting success was evidently poor at this lake, as on June 25 only six of the exposed nests seemed to have escaped the effects of predation, and the bulrushes at the other colony were so limp and deeply submerged that wind and waves had carried away all the nests there. In 1958 only the bulrush colony was occupied, but success was better, as on June 26 fifteen nests still retained eggs.

On June 11, 1958, the colony at Boyd Lake contained 12 nests built in an open growth of half-submerged tamarisk bushes at the southwest end of the reservoir.

Fossil Creek Reservoir has a less regular outline and better marshy areas than the others, and it has had by far the greatest concentration of Western Grebes. There has been little evidence of nest predation in the good cover available there. In 1957 the majority of the nests were in a large tamarisk-rimmed cattail marsh at the southwest end, with some also in a cattail-bulrush marsh at the south-east end. In 1958 and 1959, for reasons unknown, the former colony was abandoned while the latter increased greatly.

The clutch size and distribution of nests in the colonies on Fossil Creek are given in table 1. It is realized that not all the clutches were complete. These distributions are similar to those in the smaller colonies. In the large colony at Fossil Creek in 1959, three of the nests of the Western Grebe also contained single eggs of the Pied-billed Grebe (*Podilymbus podiceps*), although only one nest of the latter was found in the marsh. One nest in the colony at Timnath, in 1958, also contained an egg of the Pied-billed Grebe. In seven of the Western Grebe nests in the colony at Fossil Creek in 1958, and ten in that colony in 1959, the eggs had been covered on my approach as is done by the smaller grebes.

Nests in the various colonies ranged from one to six feet in diameter (usually 1½ to 2 feet) and were spaced from 6 to 50 feet apart, tending generally to be smaller and closer together in dense cover. They were normally massed within 100 feet of the open water. The materials used were those most easily available; weed stems and algae were used in the exposed colony at Timnath Reservoir and at

Boyd Lake, whereas cattails and bulrushes were typical at the others. The supporting mats under the nests, usually green bulrushes, were often placed on submerged snags when these were available.

In exposed colonies the grebes often left the nests while I was still several hundred yards away. They swam well out into open water where they waited, calling noisily. Where the cover was denser, however, I managed to approach within ten feet of some incubating birds.

TABLE 1
DISTRIBUTION OF CLUTCH SIZES IN WESTERN GREBE NESTING COLONIES AT FOSSIL CREEK
RESERVOIR, COLORADO

Clutch size	Number of nests	Clutch size	Number of nests	Clutch size	Number of nests
June 2, 1957		June 8, 1958		June 5, 1959	
SW end		SW end—None		SW end—None	
		SE end		SE end	
1	12	1	10	1	6
2	7	2	9	2	16
3	1	3	19	3	49
4	1	4	32	4	54
Total	21	5	35	5	11
		6	10	6	1
SE end		Total	115	Total	137
0	2				
1	5				
3	1				
Total	8				

In 1960 the reservoirs around Fort Collins failed to reach capacity by two or three feet, and there was no nesting at the known sites as the water did not flood the cover. However, grebes lingered in small numbers, and I have no doubt that nesting will be re-established when conditions permit.—DONALD G. DAVIS, *Timnath, Colorado, December 15, 1960.*

The Flight Speed of a Red-breasted Merganser.—In the course of investigating the terrestrial avifauna of the Cape Thompson area of northern Alaska for the United States Atomic Energy Commission, several low aerial reconnaissance flights of the Kupuk River (latitude 68° 22'N, longitude 166° 00'W) were made. On May 29, 1960, a flock of six Red-breasted Mergansers (*Mergus serrator*) was flushed from the river ahead of the airplane. The area in which this flock was flushed was bordered on the south by a sheer bluff, rising to about 30 feet, and on the north by a bank 4 feet high. The wind was blowing from the west at 20 miles per hour. At the time the ducks were flushed we were flying east up the river. When the ducks took flight, all the birds turned aside except one male which flew slightly below and ahead of the airplane. This bird with a burst of speed managed to keep his position in relation to the aircraft for about 1500 feet before finally losing ground and turning aside. The air speed of the airplane during the chase was 80 miles per hour. The 20 miles per hour wind from the west added to the 80 miles per hour air speed would give the bird a ground speed of 100 miles per hour.

Similar flights had been conducted several times before and although mergansers had been flushed, none behaved in such a manner that an air speed could be calculated.

Cooke (Flight Speed of Birds, U.S. Dept. Agr. Circ. 428, 1937) did not list the flight speed of the Red-breasted Merganser in her compilation of flight speeds. The fastest speed of a duck that she recorded was that of a Canvasback (*Aythya valisineria*) with a clocked speed from an airplane of 72± miles per hour.—MAX C. THOMPSON, *Arctic Health Research Center, Anchorage, Alaska, November 25, 1960.*

Notes on Bird Nests Found in a Desert Shrub Community Following Nuclear Detonations.—In the past three years I have conducted investigations in plant ecology at the United States Atomic Energy Commission's Nevada Test Site, Nye County, Nevada, under A. E. C. Contract Num-

ber AT (29-2) 517. In the course of these investigations chance observations of bird nests were recorded.

The purpose of this note is to report the occurrences of these nests in relation to the gross influences of nuclear detonations (air bursts), which occurred prior to September 2, 1957, upon the vegetation of a desert shrub community.

Nuclear explosions differ from conventional explosions primarily in the attainment of extremely high temperatures and the emission of nuclear radiations. The tremendous heat released is the primary destructive agent of vegetation and creates a large circular burn in the community. A nuclear device of nominal energy yield (approximately 20 kilotons), positioned far enough above the ground to prevent the fire ball from contacting the soil surface, is capable of destroying the vascular vegetation within a radius of 0.6 miles (table 1). The powerful shock winds produced have little apparent effect upon low growing plants beyond the limits of extensive thermal damage, although these shocks may break tall Joshua trees at distances of more than a mile.

TABLE 1

BIRD NESTS FOUND IN THE VICINITY OF A NUCLEAR DETONATION SITE,
NYE COUNTY, NEVADA, 1958, 1959, AND 1960

Distance in miles from detona- tion point	Gross damage to vegetation	Kinds and numbers of active nests found
2.5-1.3	Undamaged desert shrub community. Joshua trees (<i>Yucca brevifolia</i>), scattered. Dominant shrubs, hopsage (<i>Grayia spinosa</i>) and <i>Lycium andersonii</i> . Sparse bunch grasses, rice grass (<i>Oryzopsis hymenoides</i>), and desert needle grass (<i>Stipa speciosa</i>). Variable understory of small winter annuals, primarily <i>Chaenactis steviodes</i> .	Joshua trees Swainson Hawk (<i>Buteo swainsoni</i>), 1, 1960; eggs 2, young 2. Western Kingbird (<i>Tyrannus verticalis</i>), 1, 1960; eggs 3. Mockingbird (<i>Mimus polyglottos</i>), 1, 1960; eggs 3, young 3. Shrubs Black-throated Sparrow (<i>Amphispiza bilineata</i>), 2, 1960; eggs 3, 3.
1.3-0.7	Joshua trees broken by shock winds.	Shrubs Brewer Sparrow (<i>Spizella breweri</i>), 3, 1958; eggs 4, 3, 3, young 4, 3, 2. Black-throated Sparrow (<i>Amphispiza bilineata</i>), 1, 1960; eggs 3.
0.7-0.6	Shrubs destroyed by heat and shock but bunch grasses survive.	None found.
0.6-0	All standing vascular plants destroyed. Revegetation by annuals, primarily <i>Mentzelia albicaulis</i> and Russian thistle (<i>Salsola kali</i>).	Ground Horned Lark (<i>Eremophila alpestris</i>), 1, 1960; young 2. Concrete building House Finch (<i>Carpodacus mexicanus</i>), 1, 1960; eggs 5, young 5. Say Phoebe (<i>Sayornis saya</i>), 1, 1958, 1959, 1960; eggs 5, 5, 5, young 5, 5, 5.

The results of field observations are reported in table 1. The nest found nearest the detonation point was that of a Horned Lark (*Eremophila alpestris*). This nest was about 0.2 miles from ground zero and was discovered in April, 1960. The destruction of shrubby vegetation appears to modify the community in favor of Horned Larks. At all seasons populations of Horned Larks are greater in the disturbed area than in the adjacent shrub-dominated vegetation.—W. H. RICKARD, *Mercury, Nevada, December 20, 1960.* (Present address: Biology Laboratory, Hanford Laboratories, Richland, Washington.)

NOTES AND NEWS

The Harry R. Painton Award of the Cooper Ornithological Society for 1961 was made to Robert A. Norris and Gordon L. Hight, Jr., for their paper entitled "Subspecific Variation in Winter Populations of Savannah Sparrows: A Study in Field Taxonomy," which appeared in *The Condor* in 1957 (pp. 40-52). This award is made biennially for the paper adjudged of greatest merit and significance published in the preceding four years in the journal.

At the annual meeting of the Cooper Ornithological Society in April in Tucson, William George won the A. Brazier Howell Award for the best paper presented by a person who does not hold a doctoral degree in biology. Mr. George's paper was entitled "The Evolution of Form and Function of a Single Muscle in Birds."

Dr. Ernst Mayr has been appointed Director of the Museum of Comparative Zoology at Harvard University. He will take office on July 1, 1961, succeeding Dr. Alfred S. Romer, who is retiring from administration.

The Cooper Ornithological Society approved a change in bylaws on April 7 at its business meeting providing for the election of six members to its Board of Governors and for the retirement of inactive members of the board who have entered it by reason of service as officers of the Society's divisions. The newly elected members are: Dean Amadon, William H. Behle, Joe T. Marshall, Jr., Ernst Mayr, Robert W. Storer, and Alexander Wetmore.

The Thirteenth International Ornithological Congress will convene at Cornell University, Ithaca, New York, from June 17 to 24, 1962. The official announcement and the application for membership in the Congress are now ready for distribution. Interested persons who have not already done so should send their names and addresses to the Secretary General as soon as possible.

A small fund has been obtained to provide partial support for the travel of a few persons coming from outside North America. Application forms will be sent to persons requesting them. Citizens of the United States and Canada are not eligible.

All applications for membership, travel grants, and places on the program should be returned to the Secretary General before December 1, 1961.

—CHARLES G. SIBLEY, *Secretary General, Fernow Hall, Cornell University, Ithaca, New York, U.S.A.*

The Royal Aircraft Establishment of Great Britain at Farnborough has recently released a library translation (No. 846) of a Russian ornithological paper which should be of great interest to students of bird flight. The paper is "Aerodinamika Ptits-Paritelei" (The Aerodynamics of Soaring Bird Flight) by I. N. Vinogradov and was published by DOSARM, Moscow, in 1951. The title is somewhat misleading as the paper has little to do with soaring flight but has considerable new material on flapping flight, including numerous flight photographs. The paper is available from the Ministry of Aviation, London, W.C. 2, England.—C. D. CONE, JR.

The Josselyn Van Tyne Memorial Fund will have a sum of \$300 available for research awards at the end of the fiscal year, July 31, 1961. Any student of birds is invited to apply for part or all of this amount. Ten duplicate copies of an application are desired for distribution to members of the Research Committee who will determine how the funds will be allotted. The application should give a full description of the proposed research, the type of help required (equipment, travel, assistance, and so forth), the amount of money desired, and the background and training of the applicant. With young men or women just starting their careers, a supporting letter from one or more recognized ornithologists would be helpful.

Applications should be submitted not later than June 1, 1961.—S. C. KENDEIGH, *Vivarium Building, University of Illinois, Wright and Healey Sts., Champaign, Illinois.*

Because of persistent reports of a downward trend in the population of Bald Eagles, the National Audubon Society has launched a study aimed at determining the status of the species. This project is designed to cover at least five years and to gather data from all parts of North America. The study will consist of two parts, first, an inventory based on the number of active nests located and, second, an investigation of

various aspects of eagle biology. Information is urgently needed on the location of active eagle nests and also on wintering concentrations of eagles. If you have information on these or any other facets of eagle biology, please communicate with ALEXANDER SPRUNT, IV, Box 231, Tavernier, Florida.

PUBLICATIONS REVIEWED

THE KIRTLAND'S WARBLER. By Harold Mayfield. Cranbrook Institute of Science, Bloomfield Hills, Michigan, xvi + 242 pp., 9 figs., 8 pls., and colored frontispiece, 1960; \$6.00.

This is a research report filled with valuable information and presented in good, readable style. Truly exhaustive studies of the rare Kirtland Warbler have been pursued for many years, beginning in 1930, by Josselyn Van Tyne. From 1944 on, Mayfield was a part of the study team and it is to his very great credit that he has been able to bring the investigations to a meaningful, published conclusion.

Rare species of birds are likely to attract more attention than they deserve and more than the anticipated biological results would justify. But the Kirtland Warbler does present some special challenges and opportunities for significant results even though the total population of the species is probably less than 1000 individuals. The amazingly restricted breeding range in central Michigan and the comparably restricted winter range in the Bahama Islands invite special investigation of the factors leading to range limitation, survival, and productivity. The answers in so far as they emerge relate primarily to the breeding grounds where most of the research effort was concentrated.

The Kirtland or Jack Pine Warbler is limited in spring and summer to one small part of the range of the jack pine. The three factors suggested as contributing to this and which in combination are peculiar to the warbler's range in northern Lower Michigan are: porous soils, am-

ple ground cover, and unimpeded sweep of forest fires in the jack pines. The warbler requires extensive stands of small conifers, growing thickly, at least in clumps, and the foliage of them must reach down to the ground cover; the latter must be short but in places fairly thick and the soil must be dry and porous, for it is here that the nests are placed. By extensive correlation of environmental conditions with presence and absence of the birds, the author has been able to state the habitat requirements of the species as explicitly and dependably as has been possible for any species of passerine bird.

Chapters on territory, the nesting cycle, breeding behavior and song are rich in substantive findings and each is provided with a meaningful summary.

Although the Kirtland Warbler is a strictly territorial species, it is colonial, or perhaps better stated, it forms assemblies or settlements. Mayfield believes that "colonies" reflect a gregarious drive and that this may be beneficial in that females are aided in finding males and that there is mutual stimulation to breeding resulting from males being in communication by song; thus he tends to favor Darling's views on social stimulation.

Perhaps most significant are the chapters dealing with the influence of cowbird parasitism and with productivity and mortality. The cowbird probably invaded the breeding range of the warbler in the 1870's and became numerous there in the 1890's. Now it is calculated from survival studies that the warblers would produce 60 per cent more fledglings if there were no cowbird interference. As a consequence a pair of Kirtland Warblers at present produces only 1.4 fledglings per year. The annual survival rate for the adults of the species is about 60 per cent and the life expectancy is about two years.

This book may be regarded as a milestone in field research, representing prolonged, intensive effort, often of teams of workers, and with intelligent direction leading to clear biological results.

—ALDEN H. MILLER.

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